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STUDIES IN THE GENUS COCCOLOBA, IV. THE SPECIES FROM PUERTO RICO AND THE VIRGIN ISLANDS AND FROM THE BAHAMA ISLANDS

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NATHANIEL BRITTON and his colleagues have published treatments for the species of *Coccoloba* known from Puerto Rico and the Virgin Islands and from the Bahama Islands as parts of larger floristic works. Since both of these floras are in use today, it is desirable to present two treatments to parallel Britton's work and to bring up to date the nomenclature as well as the species definition. Since Britton's work on these island areas appeared, there have been relatively few additional collections from these areas and the need for more material of many species remains critical. A field knowledge of the species over the larger area of the West Indies has brought about a better understanding of the morphological variation represented in the areas considered in this paper. As a result, several of Britton's species have been reduced to synonymy and others have been assigned to older taxa not fully understood at the time of Britton's publication.

The species of *Coccoloba* in Puerto Rico, the Virgin Islands and the Bahamas as recognized by Britton and his colleagues are listed below with their equivalents in the present study:

<i>Coccolobis bahamensis</i>	<i>Coccoloba tenuifolia</i>
<i>Coccolobis boricuensis</i>	<i>Coccoloba swartzii</i> f. <i>urbaniana</i>
<i>Coccolobis diversifolia</i>	<i>Coccoloba swartzii</i>
<i>Coccolobis grandifolia</i>	<i>Coccoloba pubescens</i>
<i>Coccolobis klotzschiana</i>	<i>Coccoloba microstachya</i>
<i>Coccolobis krugii</i>	<i>Coccoloba krugii</i>
<i>Coccolobis laurifolia</i>	<i>Coccoloba diversifolia</i>
<i>Coccolobis northropiae</i>	<i>Coccoloba northropiae</i>
<i>Coccolobis obtusifolia</i>	<i>Coccoloba microstachya</i>
<i>Coccolobis pirifolia</i>	<i>Coccoloba pyrifolia</i>
<i>Coccolobis rugosa</i>	<i>Coccoloba rugosa</i>
<i>Coccolobis rupicola</i>	<i>Coccoloba costata</i>
<i>Coccolobis sintenisi</i>	<i>Coccoloba sintenisi</i>
<i>Coccolobis swartzii</i> var. <i>portoricensis</i>	<i>Coccoloba swartzii</i>

<i>Coccolobis uvifera</i>	<i>Coccoloba uvifera</i>
<i>Coccolobis venosa</i>	<i>Coccoloba venosa</i>

In two earlier works Baron H. F. A. Eggers published studies of the flora of St. Croix (St. Croix's Flora, 110. 1876, The Flora of St. Croix and the Virgin Islands, Bull. U.S. Nat. Museum 13: 88. 1879). I do not always agree with the species to which Britton and Wilson have assigned Eggers' species and varieties. I have seen a large number of Eggers' specimens through the courtesy of the Director of the Botanical Museum and Herbarium at Copenhagen. While Eggers cited few collection numbers in the two publications mentioned above, his annotations of specimens and the localities given can be taken to indicate the specimens he had for study. The species and varieties which Eggers cites should be referred as follows:

<i>Coccoloba diversifolia</i>	<i>Coccoloba krugii</i> \times <i>C. uvifera</i>
<i>Coccoloba laurifolia</i>	<i>Coccoloba diversifolia</i>
<i>Coccoloba leoganensis</i>	<i>Coccoloba diversifolia</i>
<i>Coccoloba nivea</i>	<i>Coccoloba venosa</i>
<i>Coccoloba obtusifolia</i>	
var. <i>jacquinii</i>	<i>Coccoloba microstachya</i>
var. <i>barbadensis</i>	<i>Coccoloba swartzii</i>
var. <i>parvifolia</i>	<i>Coccoloba microstachya</i>
<i>Coccoloba punctata</i>	
var. <i>jacquinii</i>	<i>Coccoloba swartzii</i>
var. <i>barbadensis</i>	<i>Coccoloba krugii</i> \times <i>C. uvifera</i>
var. <i>microstachya</i>	<i>Coccoloba microstachya</i>
var. <i>parvifolia</i>	<i>Coccoloba microstachya</i>
<i>Coccoloba rugosa</i>	<i>Coccoloba rugosa</i>
<i>Coccoloba tenuifolia</i>	<i>Coccoloba diversifolia</i>
<i>Coccoloba uvifera</i>	<i>Coccoloba uvifera</i>

Coccoloba P. Br. ex L. Syst. Nat. ed. 10, 1007, 1367. 1759; Taxon 3: 114, 156, 233. 1954, nom. conserv.

Guaiabara Miller, Gard. Dict. ed. 4, 2: 1754.

Coccolobis P. Br. Civ. Hist. Jam. 209, pl. 14, f. 3. 1756.

KEY TO THE SPECIES FOUND IN PUERTO RICO AND THE VIRGIN ISLANDS

Perianth lobes investing the achene; leaves usually membranaceous; ochreolar sheaths commonly elongating with the flowers; bracts usually black in color. *C. venosa*.

Hypanthium investing the achene, the perianth lobes appressed against the apex of the achene or coronate on the achene; leaves coriaceous to fleshy, rarely membranaceous; ochreolae not elongating with the flowers but broken early; bracts usually straw colored or brown.

Pedicels shorter than the ochreolae in flower and in fruit.

Leaves of normal shoots characteristically 2-5 cm. long.

Leaves ovate, cordate at the base, greenish tan in color even when fresh; venation inconspicuous above, primary veins evident by color

below; nodes swollen and bead-like when fresh but only slightly larger than internodal diameter when dry; fruit 4–5 mm. long, strongly triangular in cross section *C. krugii*.
 Leaves ovate-oblong, normally rounded at the base and not cordate, dark brown to black on drying; primary and secondary veins conspicuous on both surfaces, densely reticulate; nodes bead-like, swollen and conspicuously larger than the internodal diameter when dry; fruit round in cross section, not angled. *C. microstachys*.

Leaves of normal shoots characteristically 7–12 cm. long.

Leaves normally ovate-lanceolate; venation mostly inconspicuous on both leaf surfaces; blades characteristically and conspicuously lighter in color below when dry; fruit globose, ca. 4 mm. in diameter. *C. pyrifolia*.
 Leaves mostly broadly ovate to elliptic; primary veins conspicuous on both surfaces, secondary venation finely reticulate, evident but not conspicuous; blades only slightly lighter in color below; fruit ovoid, 8–10 mm. long, 6 mm. diameter.

Leaves thick and fleshy when fresh, heavy and coriaceous when dry; inflorescence axis stout, the flower clusters often appearing to be sunken in the axis. *C. swartzii* f. *urbaniana*.
 Leaves not evidently thick and fleshy, when dry only thinly coriaceous; inflorescence axis not fleshy, the flower clusters not imbedded in the axis. *C. swartzii*.

Pedicels longer than the ochreolae in flower and in fruit.

Leaves large, usually 25 cm. wide or more.

Leaves bullate between the primary veins, glabrous, the basal lobes of the blade often surrounding the stem; stem angled or keeled, when dry conspicuously so; inflorescence red. *C. rugosa*.
 Leaves reticulate but not bullate, pubescent at least when young; stems not evidently angled; inflorescence not noticeably red in color. *C. pubescens*.
 Leaves smaller, usually less than 10 cm. wide, rarely 15–20 cm. wide, never strongly bullate or with lower leaf surface deeply chambered by the protruding veins.

Leaves suborbicular, thick and fleshy, one basal lobe of the blade usually overlapping the petiole; fruit obpyriform 1.2–2 cm. long. *C. uvifera*.

Leaves ovate to elliptic or obovate.

Fruit obpyriform, broadest above the middle; leaves with one basal lobe slightly overlapping the petiole. *C. uvifera* \times *C. krugii*.
 Fruit broadest below the middle; leaf bases variable but without a basal lobe overlapping the petiole.

Inflorescences with 10 to 20 pistillate flowers or clusters of staminate flowers. *C. diversifolia*.
 Inflorescence with 50 or more pistillate flowers or clusters of staminate flowers.

Inflorescence and flowers red, pedicels 4-5.5 mm. long. *C. sintenisii*.
 Inflorescence and flowers usually green, not bright red; pedicels 1.5 mm. long.
 Primary venation conspicuous, secondary venation inconspicuous. *C. costata*.
 Primary venation and secondary venation conspicuous, finely reticulate. *C. uvifera* × *C. krugii*.

Coccoloba venosa L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Jour. Bot. 51: 123. 1913; Britton & Wilson, Sci. Surv. P.R. 5: 269. 1924; Howard, Jour. Arnold Arb. 30: 398. 1949.

Coccoloba punctata L. Sp. Pl. ed. 2, 523. 1762.

Coccoloba nivea Jacq. Hist. Stirp. Amer. 115, pl. 78. 1763; Enum. Pl. 19. 1762.

Trees to 10 m. tall; branches terete, glabrous, the nodes not tumid; ochreæ membranaceous, deeply cleft, acuminate on one side, or truncate, to 2 cm. long, glabrous or with flattened glands; leaf blades oblong-lanceolate to elliptic, the apex short acuminate, the base narrowed and slightly cordate or cuneate or obtuse, 8 × 4, 10 × 4.5, 16.5 × 6.5, 21 × 9, 27 × 10.5 cm. long and broad, membranaceous, glabrous except for clusters of hairs in the axils of the veins, sparsely glandular below; midrib and primary veins slightly prominent on both surfaces, the primary veins 8-13 pairs, straight or arcuate, bifurcate and anastomosing at the margins, the petioles 5-10 mm. long, glabrous; leaves of the adventitious shoots about the same size, the internodes much elongate and the ochreæ to 4 cm. long; inflorescence terminal or terminal on short lateral branches, the rachis puberulent, angular; staminate flowers in clusters of 2-5, the pistillate flowers solitary, the bracts lanceolate-ovate, to 1.5 mm. long, black, puberulent to pilose or commonly with a fringe of hairs at the apex; ochreolæ membranaceous, enlarging with the expanding bud, each flower with an ochreola, to 2 mm. long, the flowering pedicels 1-2 mm. long, glabrous; hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5-2 mm. long and broad, slightly unequal, the fertile stamens to 1 mm. long; fruiting pedicels 1.5-2.5 mm. long, the fruit broadly ovoid, the perianth lobes fleshy, white or pink, enclosing the black achene, the hypanthium scarcely evident in the fruit, the fruit 3-4 mm. long and broad.

DISTRIBUTION: Cuba (introduced), Jamaica (in literature but no specimens have been located), Hispaniola, Puerto Rico and the Virgin Islands, and the Lesser Antilles to Trinidad and Tobago.

Puerto Rico: Aybonito to Buenvista de la Plata, *Sintenis* 2083 (GH, US); Cayey, *Sintenis* 2215 (NY); Coamo Springs, *Britton & Cowell* 1329 (NY, US), *Goll* 653 (US), 737 (US); Comerio, *Johnston* 920 (NY); Guanica, *Britton & Shafer* 1891 (NY, US); Gurabo, *Stevenson* 2899 (US); Humacao, *Sargent* 3014 (US); Las Pijeras, *Britton, Britton & Marble* 2219 (NY, US); Ponce to Coamo,

Heller 509 (NY, US); Ponce to Juana Mata, Goll 805 (US); Ponce to Santa Isabel, Britton & Britton 7342 (NY); Pumula, Sargent 9133 (NY); Sardinera, Britton, Cowell & Hess 1787 (NY); Yabucoa, Eggers 425 (B, GH); Yuncos, Sintenis 1942 (B, F, GH, MO, NY, S, US); without specific location, Wydler 347 (NY), Schwanecke s.n. (B). **Vieques Island:** Isabel Segunda, Shafer 2450 (NY, US). **St. Croix:** Crequis, Eggers s.n. (US); Caledonia Gut, Eggers s.n. (NY); Christiansted, Quinn 1130 (NY); Northside Belvidere, Ricksecker 456 (F, GH, MO, NY, US); Prosperity Hills, Eggers s.n. (A); without specific location, Oersted s.n. (US). **St. Thomas:** Collections by Crudy, Eggers, Forstrom and Oersted without specific location or collection numbers. **Tortola:** Sage Mt., J. S. Beard 330 (A, MO); Sea Cow Bay, Shafer 1125 (F, NY, US).

Beard reports this species to be called "Trible Grape" on Tortola while it is commonly known as Chiggery Grape and Calambreña in Puerto Rico.

Britton and Wilson list *Coccoloba excoriata* L. as a synonym of this species in their treatment of the genus. The Linnean species, however, is properly referred to *C. tenuifolia* L. See Howard Jour. Arnold Arb. 28: 92-95. 1957.

Coccoloba krugii Lindau, Engler Bot. Jahrb. 13: 145. 1890, Symb. Antill. 1: 222. 1899; Britton & Wilson, Sci. Surv. P.R. 5: 267. 1924; Howard, Jour. Arnold Arb. 37: 337. 1956.

Coccoloba børgesenii Schmidt, Fedde Repert. Sp. Nov. 24: 75. 1927.
Coccoloba børgesenii forma *ovato-lanceolata* Schmidt, Fedde Repert. Sp. Nov. 24: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly geniculate and nodose; ochrea membranaceous, persistent, 3-5 mm. long; petioles borne at the base of the ochrea, corky at the base, 5-6 mm. long; blade ovate to suborbicular 2×1.8 , 4×3.5 , 5×4 cm. long and broad, thin-coriaceous, glabrous or rarely with a few hairs near the attachment of the petiole, the margin flat or recurved, the midrib flat above slightly prominent below, the primary veins 4-6 pairs, straight, bifurcating and anastomosing near the margin, flat on both surfaces, the secondary venation minutely reticulate below, smooth above, the apex obtuse or rounded, the base cordate or rounded; adventitious leaves from the base of the 1 cm. long ochrea with petioles 1 cm. long and blades cordate or elliptic to 7×6 cm. long and broad; inflorescence terminal, 5-8 cm. long, rachis glabrous, the staminate flowers 1-3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ochreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ochreolae, the hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 1.5 mm. long; fruit ovoid or angularly fusiform, strongly triangular in outline, 4-5 mm. long, 3-3.5 mm. in diameter, the perianth lobes appressed, above half the length of the fruit.

DISTRIBUTION: Bahamas, Haiti, Dominican Republic, Jamaica, Puerto Rico, Anagada, Antigua, Barbuda, St. Martin.

Puerto Rico: Guanica near Salinas, *Britton, Britton & Boynton* 8314 (NY); Guanica in woods on Monte Cobana, *Sintenis* 3776 (MO, NY); Ponce, *Underwood & Griggs* 673 (NY, US); *Heller* 6211 (A, F, GH, MO, NY, US); *Britton & Cowell* 1289 (NY, US); Icacos Cay, *Britton* 7153 (NY); Vieques Island, *Shafer* 2785 (NY, S, US); Guayanilla, *Britton & Shafer* 1841 (F, MO, NY, US). **Anagada:** *Fishlock* 26 (NY), 27 (NY); *Britton & Fishlock* 1001 (NY), 1063 (F, NY, MO, US), *J. Beard* 323 (A).

Coccocloba krugii Lind. \times **C. uvifera** L., hybr. nov.

Shrub of 6 feet or small tree; young branches terete, striate, puberulent to pubescent; ochrea membranaceous, oblique and slightly flaring at the apex, 1–1.5 cm. long, puberulent to pubescent; leaves of normal shoots on petioles 7–10 mm. long, blades ovate to ovate-elliptic, apex obtuse to broadly rounded, rarely acuminate with an obtuse point, the base oblique, cordate to rounded, one basal lobe often overlapping the petiole, 6 \times 3, 8 \times 6, 11 \times 8 cm. long and broad, the midrib and veins prominent below, sub-prominent above when dry, ultimate venation reticulate, primary veins 6–7, arcuate and anastomosing near the margin, 2–3 veins close to the base of the blade; leaves of adventitious shoots on petioles 7–10 mm. long, the blades ovate, ovate-elliptic or rarely ovate-lanceolate, 14 \times 8 to 29 \times 18 cm. long and broad; inflorescence simple, terminal to 20 cm. long, the rachis slender, puberulent becoming glabrate; bracts broad, triangular ovate, puberulent, the ochreolae membranaceous, to 1 mm. long, puberulent, the pedicels shorter than the ochreolae; staminate flowers 2–4 per node, the pistillate flowers solitary at the nodes, hypanthium to 1 mm. long, perianth lobes orbicular, 1.5–2 mm. long and broad, filaments of fertile stamens 2 mm. long; pedicels in fruit equal to twice the length of the ochreolae, fruit fusiform to fusiform-ovoid, 11 mm. long, 8 mm. in diameter, the perianth lobes not coronate.

Puerto Rico: Morrillos de Cabo Rojo, *Britton, Cowell & Brown* 4709 (F, NY, US); Ponce, *F. H. Sargent* 564 (US). **St. Croix:** La Vallee, *Ricksecker* s.n. (F); Oxholmia, *Borgesen* (C); Rustup Twist, *Ricksecker* 465 (F, GH, MO, NY, US); Saltpond, *Raunkiaer* s.n. (C); *Eggers* without location or number (C). **St. Thomas:** without specific location or number: *Eggers* (US), *Ehrenberg* (B), *Raunkiaer* (C); *Holdridge* 122 (NY). **Little St. James:** *Britton & Rose* 1407 (NY, US). **St. Jan:** *Raunkiaer* s.n. (C). **Virgin Gorda:** *Fishlock* 286 (GH), 353 (NY, US); *A. C. Smith* 10563 (A).

Judging from the variety of determinations which exist on the specimens cited above, the plants representing this hybrid swarm have caused difficulty to other taxonomists. In addition to the citations given, I have seen thirty-five other sheets with data as to locality, collector, or collector's number, which are insufficient to allow citation. Twenty-five such sheets from the Copenhagen herbarium are old collections obviously from the one-time Danish possessions in the West Indies. These specimens present a range of variation which includes the often diverse forms represented in the collections cited.

The majority of the specimens assigned to this hybrid population were sterile and represented portions of adventitious shoots. Some attached or associated fertile branches gave the impression of unusually large specimens of *Coccoloba krugii* through the long and tenuous inflorescence and through the fruit. In all but two collections the pedicels in both flower and fruit were short. A few specimens had associated fruits resembling those of *C. uvifera*.

Two collections from Virgin Gorda are referred to this hybrid population. One was made by W. C. Fishlock from the "mountain" and a more recent collection by A. C. Smith was more adequately described as a tree, 4–5 m. tall in low thick woods at the summit and on the eastern slope of Virgin Peak at an altitude of 150–420 m. These two collections represent a heavy and fleshy phase of the hybrid. They seem to bear the same relationship to the hybrid population as *C. swartzii* forma *urbaniana* does to *C. swartzii* on the mainland of Puerto Rico. The Fishlock material is in flower and the Smith specimen in fruit. Both specimens are gnarled in appearance and on both the leaves are variable in shape but predominantly broadly ovate. The apparent thickness or leathery appearance of the blades is striking. The apex is rounded and emarginate and the base strongly obliquely cordate. Representative leaves are 6.5×5 to 10.5×8 cm. long and broad. The venation is conspicuous on both surfaces and the ultimate venation coarsely reticulate. The inflorescence slightly exceeds the length of the leaves and the plants are dioecious. The pedicels of both the flowers and fruits in the collections by Fishlock and Smith are 1.5–2 mm. long. In the other collections cited the pedicels in flower and fruit are 1 mm. in length but appear smaller in contrast. Fishlock reported the common name of "white grape" for this plant on Virgin Gorda, while *C. uvifera* is known as "sea grape" and *C. krugii* as "white wood."

Coccoloba microstachya Willd. Sp. Pl. 2: 459. 1800; Lindau, Engler Bot. Jahrb. 13: 146. 1890.

Coccoloba parvifolia Poir. in Lam. Encycl. 6: 64. 1804.

Coccoloba klotzschiana Meisn. DC. Prodr. 14: 155. 1856; Lindau, Engler Bot. Jahrb. 13: 148. 1890.

Coccoloba microstachya var. *ovalifolia* Meisn. DC. Prodr. 14: 162. 1856.

Coccoloba microstachya var. *lanceolata* Meisn. DC. Prodr. 14: 162. 1856.

Coccoloba punctata Griseb. in part, Flora Brit. W.I. 163, 1859, not Linnaeus.

Coccoloba microstachya var. *rotundifolia* Urban ex Lindau, Engler Bot. Jahrb. 13: 147. 1890.

Coccoloba obtusifolia Lindau, Symb. Antill. 1: 222, 1899; Britton & Wilson, Sci. Surv. P.R. 5: 268. 1924, not Jacquin.

Shrub or tree to 20 feet tall; branches terete, the nodes tumid, pubescent or with hair primordia, the bark gray to tan in color; ochrea membranaceous, cylindrical, pubescent, 4 mm. long; petioles 3–6 mm. long, flattened above, normally pubescent; blades variable in size and shape, ovate, ovate-lanceolate, oblong or elliptic, 3.5×1.5 , 4×2 , 5.5×3.5 to 7×4 cm.

long and broad, thin-coriaceous, usually turning black on drying, the margin entire, often undulate, sometimes tightly recurved; midrib and veins prominent on both surfaces, forming a dense reticulum, although blades relatively thick and often somewhat fleshy in fresh condition, the veins 7-9 pairs, prominent or numerous and all equal and less conspicuous, straight or arcuate, curved and anastomosing at the margin; glabrous above, pilose or glabrate below, occasional hairs remaining on the veins or rarely the entire leaf surface persistently pubescent; apex acute, acuminate rounded or emarginate, the base narrowed, rounded or slightly cordate; leaves of adventitious shoots ovate-lanceolate, 10.5×5.5 to 16.5×5 cm. long and broad on petioles 7 mm. long with ochreae 8 mm. long, the adventitious leaves cordate at the base, generally tapering or acuminate at the apex and often conspicuously puberulent below; inflorescence terminal, 5-10 cm. long, the rachis usually pubescent, tenuous, rarely stout, often geniculate, commonly recurved; staminate flowers two, rarely one or more than two at the nodes; pistillate flowers solitary, the bracts broadly ovate, 0.5 mm. long, puberulent; ochreolae membranaceous, puberulent, to 0.5 mm. long, erect and surrounding the flower in the staminate plants, generally appressed or flattened against the rachis in the pistillate plants in flower and fruit, pedicels none or shorter than the ochreolae, the hypanthium less than 1 mm. long, the perianth lobes 1-1.5 mm. long and 1 mm. wide; fruit sessile, generally ovate with distinctly coronate perianth lobes, to 6 mm. long and 4 mm. in diameter.

DISTRIBUTION: Dominican Republic, Puerto Rico, St. Thomas, St. Jan, Tortola, Virgin Gorda, Anguilla and St. Croix.

Puerto Rico: Guayanilla: *Britton & Shafer* 1817 (F, GH, NY, MO, US); *Sintenis* 4868 (MO, US); Guanica, *Britton & Britton* 9594 (S), *Sintenis* 3707 (B), 3431 (MO, US), *Gregory* 181 (NY), *Holdridge* 181 (A); Mayaguez, *Heller* 4546 (A, B, E, F, GH, NY, Mich. MO, NY, US), *Britton, Cowell & Brown* 4359 (NY, US), *Britton & Hess* 2715 (F, NY, US); Ponce, *Heller* 6128 (A, E, F, GH, MO, NY, US), *Underwood & Griggs* 686 (NY, US); Cabo Rojo, *Sintenis* 545 (GH, S, US), *Veles* 1096 (NY); Cayo Muertos, *Britton, Cowell & Brown* 4999 (NY); Punta Guaniquilla, *Britton, Cowell & Brown* 4566 (F, GH, NY, US), 4573 (NY, US); Rincon, *Sintenis* 5498 (F, NY), 5543 (E, F, NY); Coamo, *Sintenis* 3328 (E, GH, S, US); Peñon, *Shafer* 1985 (NY, US); Cerro Ventana, *Shafer* 2976 (NY, US); Santa Maria to Caballo Colorado, *Shafer* 2689 (NY, US); Enseñada Hondo, *Britton & Britton* 9645 (NY). **Culebra Island:** *Britton & Wheeler* 8A (NY, US), 32 (F, NY, US). **Mona Island:** *Stevens* 6170 (NY), 6213 (NY), *Britton, Cowell & Hess* 1710 (NY). **Vieques Island:** *Shafer* 2805 (NY, US). **St. Thomas:** Bolongo Hill, *Eggers* 160 (C, S); Flaghill, *Eggers s.n.* (US); Bordeaux, *Britton & Marble* 1378 (C, F, NY, US), *Ostenfeld* 328 (C), 330 (C). Without specific location: *Eggers* 135 (B), 124 (GH), 714 (A), *Britton, Britton & Shafer* 159 (C, F, NY, US), *Paulsen* 146b (NY). Collector not specified: Herb. Kunth, type of *C. klotzschiana*. **St. Jan:** Bethania, *Britton & Shafer* 192 (NY, US); Solomon's Bay, *Eggers* 3314a (C). **Tortola:** *Fishlock* 124 (F, NY). **Virgin Gorda:** *Fishlock* 20 (GH, NY), 279 (GH, US). **Anguilla:** *Boldingh* 3483b (NY). **St. Croix:** Oxholmia, *Borgesen* 64 (C); Fair Plains,

Eggers s.n. (C); Kingshill *Eggers s.n.* (C); Salt River, *Paulsen* 264 (C); Folly Hill, *Raunkiaer s.n.* (C); Rustup Twist, *Mrs. J. J. Ricksecker* 365 (F, MO, US); Salt River Cliff, *A. E. Ricksecker* 459 (F, GH, MO, NY, US); Christiansted, *Rose, Fitch and Russell* 3582 (NY, US); Anna's Hope, *Thompson* 398 (GH, NY); Mt. Eagle, *Thompson* 434 (GH, NY).

The holotype of this species is *Willdenow* 7703 in the Willdenow Herbarium in Berlin. In his original monograph of this genus, Lindau accepted *Coccocloba microstachya* Willd. and recognized three varieties. *Coccocloba microstachya* var. *ovalifolia* was described earlier by Meisner and included the holotype. *Coccocloba microstachya* var. *lanceolata* was described also by Meisner. Lindau describes a variety *rotundifolia* attributed as a manuscript name by Urban. In the synonymy of *C. microstachya* var. *ovalifolia*, Lindau cites *C. obtusifolia* Jacquin. The two specimens in the Willdenow Herbarium in Berlin are 7703, the type of the species, and 7702, the type of *C. microstachya* var. *lanceolata* Meisner. Both are probably from St. Croix and were probably collected by Vahl. Although Lindau listed four Sintenis collections from Puerto Rico, he failed to cite a type when he described *C. microstachya* var. *rotundifolia*.

In a later treatment of the genus for the West Indies (Symb. Antill. 1: 222. 1899), Lindau recognized the earlier publication of the Jacquin name *Coccocloba obtusifolia* and, accepting this as the correct name for the species, listed in synonymy *C. microstachya* and the three varieties recognized in his earlier publication. The rejection of the morphological varieties is based on a better understanding of the variation within this species and particularly within the development of an individual plant. I agree with Lindau's concept of the morphology of the species, but cannot agree with his acceptance of the name *C. obtusifolia* Jacquin. The description and illustration of the plant Jacquin considered *C. obtusifolia* is clearly not the same plant called *C. microstachya* and typified by the Willdenow specimens. Further, *C. obtusifolia* Jacquin is based on a plant from Carthagena in Colombia. This is the plant which Lindau describes as *C. billbergii* (Engl. Bot. Jahrb. 13: 219. 1890) and this species is not known from the West Indies.

Although Willdenow described *Coccocloba microstachya* as having glabrous leaves and stems, the type specimen in the Willdenow herbarium shows a minute but distinct pubescence. In the large number of specimens examined in the herbarium and in the field, the amount and the evidence of the indument varies. The pubescence is often represented only by bases of hairs recognized as clear, lighter colored dots or cells in the epidermis of the dried leaves. Generally a slight pubescence remains on the rachis of the inflorescence and is evident when all other portions of the specimen are glabrous. The extreme in foliar pubescence was seen on a specimen collected by Boldinck (3483B) from Anguilla where the lower leaf surface of the mature foliage was almost tomentose.

The variation in leaf shape is great, not only in populations but in individual plants. The three taxa which Lindau recognized in 1890, as he

reported later, can be found on a single plant or in a single collection. Within the fourteen sheets of the four Sintenis collections that I have examined, all three varieties can be recognized. Some of the herbarium specimens cited seem to have been selected deliberately in the field to show gross and exaggerated variations. The largest adventitious leaves are on the specimens from St. Croix and many of the collections consist only of such shoots and leaves. However, a Britton & Wheeler collection (32) shows both the large leaves of the adventitious shoots as well as the smaller leaves, presumably of the same plant although no mention is made of this in the field notes.

Several specimens from St. Croix show an almost teratological thickening of the inflorescence axis. While this is common in other species, and particularly in *Coccoloba swartzii*, it appears unusual in *C. microstachya*.

Coccoloba parvifolia Poir. is based on a Vahl collection and the type is in the Jussieu Herbarium. I have examined a photograph of the type sheet and agree that this species can be referred to the synonymy of *Coccoloba microstachya* Willd. Meisner, however, recognized this species and considered it an "obscure" species from South America. However, the Vahl collection is probably from St. Croix.

The type specimen of *Coccoloba klotzschiana* in the De Candolle Herbarium at Geneva and the fragment of this in the herbarium of the New York Botanical Garden indicate this species may also be referred to *C. microstachya*.

In the extreme forms of *Coccoloba microstachya*, it is difficult to distinguish between this and *C. swartzii*. Usually, however, *C. swartzii* may be recognized by the larger leaves, longer and thicker inflorescence axes, tapered fruit with imbricated perianth lobes, the lack of pubescence (except in *forma pubescens*) and the darker, almost black color of the leaves when dry. By comparison, *C. microstachya* has smaller leaves, tan to brown in color rather than black, exaggerated tumid nodes, shorter and more tenuous inflorescences and fruit with coronate perianth lobes.

***Coccoloba pyrifolia* Desf. Cat. Hort. Paris ed. 3, 69, 389. 1829; Howard, Jour. Arnold Arb. 37: 335. 1956.**

Coccoloba pyrifolia Lindau, Engl. Bot. Jahrb. 13: 144. 1890, Symb. Antill. 1: 222. 1899.

Coccolobis pyrifolia Lindau, Brit. & Wils. Sci. Surv. P. R. 5: 267. 1924.

Coccoloba kunthiana Meisner, DC. Prodr. 14: 166. 1857.

Coccoloba punctata var. *jacquini* Griseb. Fl. Brit. W. I. 163. 1859.

Shrub of 9 ft. to a tree of 30 ft.; trunk to 14 inches diameter at breast height; branches striate, glabrous, the nodes not conspicuously swollen; ochrea subcoriaceous, glabrous, shriveling rather than deciduous, 1 cm. long; petiole inserted below the ochrea, glabrous, 0.6–1.5 cm. long; blade ovate-lanceolate, broadly ovate or occasionally completely orbicular, 4.5 × 2.5, 9 × 5, 12 × 6 cm. long and broad, coriaceous, glabrous, opaque to almost shining, the margin entire, sometimes recurved, the midrib

slightly evident below, prominent above, the primary veins flat, slightly impressed above, very slightly evident below, the secondary venation obscure, the apex obtuse, acute or rarely acuminate, the base rounded, narrowed or sub-cuneate; inflorescence terminal, spike-like, 1-2 times the length of the leaf or terminal on lateral shoots, 8 to 31 cm. long, glabrous, the staminate and pistillate flowers borne singly, the bracts triangular to 1.5 mm. long, the ochreolae membranaceous, equaling the bracts; pedicels wanting; hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 3 mm. long; fertile pistil to 2.5 mm. long; fruit globose, ca. 4 mm. in diameter, rounded at the base, obscurely 3-angled, the perianth lobes coronate, laxly acuminate; achene tan in color.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Mayaguez, Cowell 730 (F, US), 731 (F, NY, US), Otero & Alvarez 540 (A, F), Sintenis 1018 (BM, US), Heller 4560 (A, E, F, GH, Mich., MO, NY, US); Sierra de Luquillo, Sintenis 1405 (F, MO, S), 1501 (BM, GH, NY, US), Britton & Bruner 7551 (NY); Santurce, Heller 614 (F, NY, US), 1259 (F, NY), 1268 (NY, US); La Estancita, Eggers 1173 (US); Mt. Alegrillo, Britton, Stevens & Hess 2572 (F, MO, NY, US), Sintenis 238 (GH, MO, S, US), Hess 645 (NY); Vega Alta, Britton, Britton & Brown 6796 (F, NY, NEOTYPE; US); Camuy, F. H. Sargent B-200 (US); Guayamo, Britton, Britton & Brown 6544 (F, NY, US); Martin Peña, J. R. Johnston 1867 (NY, US); Mt. Morales, Britton & Marble 1058 (NY, US); Maricao, F. H. Sargent 397 (US); Bayamon, Sintenis 990 (BM, GH, US), Britton, Britton & Boynton 8455 (GH, NY, US); Lago San Jose, Hioram 372 (NY); Vega Baja, Stevens 1932 (NY); Yauco, Indiera Baja, Britton & Britton 7227 (NY); Cayey, Otero 730 (A, NY); Espinosa above Toa Baja, Britton & Britton 9709 (NY); San Juan, Gerhart & Holdridge 536 (NY); Cataño, Britton, Britton & Brown 6980 (NY); Sierra de Naguabo, Shafer 3480 (NY); Toro Negro, Doña Juana, Gregory 54 (NY).

Coccoloba pyrifolia Desfontaines was described in the third edition of the catalogue of plants in the botanic garden at Paris and was based on material under cultivation there. The origin of the plant is given as the warmer Antilles. No holotype exists for this species and no lectotype has been selected, to the best of my knowledge. There is in the herbarium at Geneva a specimen without collector's name or date, bearing a label indicating its origin as "hort. paris." It is possible that this specimen represents the original material cultivated and described in 1829 and could possibly be considered as the type. It seems more desirable to select a neotype from more recent collections and so Britton, Britton & Brown 6796 is designated the type collection, and is deposited at the New York Botanic Garden herbarium. The species has been reported from Puerto Rico, St. Thomas, Cuba and Jamaica. I have seen the collections which Lindau cited from the herbaria at Berlin and Göttingen and there are currently no collections from St. Thomas. Lindau's reference to the occurrence of this species on St. Thomas cannot be checked. Likewise the Wilson specimen from Jamaica which Lindau states is in the Grisebach Herbarium cannot be located. Fawcett & Rendle repeat this reference

which cannot be verified. The two collections by Charles Wright from Cuba which Sauvalle refers to this species in his *Flora Cubana* (139. 1873) are *Wright 2253* which is *Coccoloba praecox* Wright ex Lindau and *Wright 2256* which is the type of *C. reflexa* Lindau. It appears that *C. pyrifolia* is currently limited to Puerto Rico. The original spelling of the specific name is retained in this treatment, although all recent authors have preferred to use *Coccoloba pififolia*.

Meisner's original description of *Coccoloba kunthiana* contains few diagnostic characters and is clearly referable to the synonymy of this species. I have seen specimens in the De Candolle Herbarium on which Meisner's species is based and conclude that the differences recognized by various authors in the past have been primarily of growth characters. The plants with older and shorter compacted branches are named *C. kunthiana* and are similar to Meisner's type. These specimens also have smaller ovate leaves which are generally obtuse at the apex. Specimens from obviously faster growing shoots have larger leaves which are acute or acuminate at the apex and possess longer inflorescences. These specimens, almost without exception, have been referred to *C. pyrifolia*. It is quite clear from a study of the material cited and from a field knowledge of the species that only a single taxon is represented and that the larger acute leaves are produced on adventitious or vigorously growing shoots.

Coccoloba pyrifolia is easily recognized by the long thin inflorescences with sessile flowers. It is most easily distinguished from *C. swartzii* by having leaves which dry dark brown and almost shiny above and light brown or tan beneath and which have very inconspicuous venation.

Coccoloba swartzii Meisner, DC. Prodr. 14: 159. 1856; Lindau, Engler Bot. Jahrb. 13: 157. 1890; Howard, Jour. Arnold Arb. 30: 420. 1949, 37: 324. 1956.

Coccoloba swartzii var. (?) *portoricensis* Meisn., DC. Prodr. 14: 160. 1856; Lindau, Engler Bot. Jahrb. 13: 157. 1890; Britton & Wilson, Sci. Surv. P.R. 5: 270. 1924.

Coccoloba barbadensis Lindau, Engler Bot. Jahrb. 13: 148. 1890, not Jacq. *Coccoloba diversifolia* Lindau, Symb. Antill. 1: 223. 1899; Britton & Wilson, Sci. Surv. P.R. 5: 267. 1924.

Uvifera swartzii Ktze., Rev. Gen. 2: 562. 1891.

Coccoloba neglecta Fawcett & Rendle, Jour. Bot. 51: 124. 1913; Flora Jam. 3: 116. 1914.

Coccoloba punctata Grisebach, Krebs, Eggers, and Northrop, not Linnaeus. *Coccoloba coronata* of Millspaugh, not Linnaeus.

Trees 8–20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ochrea 10–12 mm. long, the basal portion 3–5 mm. long, coriaceous, persistent, the upper portion 5–7 mm. long, membranaceous, deciduous, puberulent to glabrate; petiole attached at the base of the ochrea, 10–18 mm. long, puberulent or glabrate; leaf blades ovate to elliptic, 2.2×1.3 , 7×5 , 11×9 , 15×7.5 cm. long and broad,

entire, coriaceous, usually turning black on drying, glabrous, pit-like depressions on the upper surface, small glands on the lower surface, the midrib and veins inconspicuous or flat above, prominent below, the primary veins 6 or 7 pairs, arcuate anastomosing, secondary venation conspicuous, reticulate, the apex acute, often rounded, the base narrowed, rounded or slightly cordate, usually oblique; leaves of adventitious shoots on petioles 1.5–2.5 cm. long, the blades generally ovate to lanceolate, 23×8.5 , 45×18.5 to 70×25 cm. long and broad, the apex acute to acuminate, the base rounded; inflorescence terminal, 10–15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3–5 flowers with tightly concentric membranaceous ochreolae forming a truncate cylinder after the flowers have fallen; pistillate flowers solitary, the ochreolae erect in flowers, flattened against the rachis in fruit, the bracts ovate, 1–1.5 mm. long, the ochreolae membranaceous 1–1.5 mm. long, the flowering pedicels shorter than the ochreolae, the hypanthium 0.5 mm. long, the perianth lobes 1–1.5 mm. long, the fertile stamens with filaments 1 mm. long; fruit ovoid 8–10 mm. long, 6 mm. in diameter, the perianth lobes 1–1.5 mm. long coronate in fruit.

DISTRIBUTION: Jamaica, Bahamas, Dominican Republic, Puerto Rico, St. Croix, Vieques Island, St. Jan, Virgin Gorda, St. Thomas, Saba, St. Kitts, Montserrat, Antigua, Guadeloupe, Dominica, Martinique, St. Lucia and Barbados.

Puerto Rico: Lago San Jose, *Hioram* s.n. (NY); Maricao, *Sintenis* 258 (B, GH, MO, NY, S, US); Dorado, *Britton, Britton & Brown* 6741 (F, NY); Cayey to Aibonito, *Britton & Britton* 9630 (NY); Monte Montoso, *Britton & Cowell* 4125 (F, NY, US); La Estancita, *Eggers* 1193 (US); Santurce, *Heller* 4666 (A, F, GH, Mich., NY, US). **St. Croix:** Salt River, *Thompson* 580 (US); Sandy Point, *Raunkiaer* 2508 (C); Jolly Hill, *Raunkiaer* s.n. (C); Mt. Eagle, *Thompson* 427 (G, NY); Signal Hill, *Ricksecker* 448 (F); Water Gut, *Isert* s.n. **Vieques Island:** *Shafer* 2733 (NY, US). **St. Jan:** Mt. Eagle, *Ravn* s.n. (C). **Virgin Gorda:** *Fishlock* 126 (NY). **St. Thomas:** *Oersted* s.n. (US).

A full discussion of the identification of *Coccoloba swartzii* Meisner and the application of the name *Coccoloba barbadensis* Jacquin was published in the Journal of the Arnold Arboretum as the second paper in this series (37: 317–339. 1956). Specimens from Puerto Rico now assigned to this species would previously have been referred to *C. swartzii* var. *portoricensis*, being intermediate in all characters between the typical expression of *C. swartzii* from Jamaica, the type locality, and *C. swartzii* var. *urbaniana* (*C. borinquensis* Britton). The specimens from St. Croix and other of the Virgin Islands are unlike the few plants from Puerto Rico and more similar to specimens from the Lesser Antilles. Considering the species as it occurs in many populations from Jamaica and Hispaniola south to Barbados and St. Lucia, there is no question that the Puerto Rican specimens are only slight variations in a greater range and should be included in the typical variety of *C. swartzii*.

In their studies for the Flora of Puerto Rico, Britton and Wilson assigned these specimens to *C. diversifolia* Lindau. I have already pointed out the general misapplication of this name (Jour. Arnold Arb. 30: 421. 1949).

Coccoloba swartzii forma *urbaniana* (Lindau) Howard, Jour. Arnold Arb. 37: 328. 1956.

Coccoloba urbaniana Lindau, Engler Bot. Jahrb. 13: 155. 1890 in part, Symb. Antill. 1: 225. 1899.

Coccolobis borinquensis Britton, Sci. Surv. P.R. 5: 267. 1924.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Sierra de Naguabo, Loma Icaco, Shafer 3448 (NY, TYPE of *C. borinquensis*), Britton, Britton & Cowell 207 (NY); Sierra de Luquillo, Sintenis 1527 (F, GH, HOLOTYPE; MO, NY, S, US), Wilson 213 (F, NY, US), Gregory 56 (NY), Britton & Bruner 7665 (NY), 7676 (NY), Barbour & Gerhart 9729 (NY); Indiera Baja, Britton & Britton 7228 (GH, NY, US); Camp Dona Juana, Villalba, Gregory 64 (NY); Maricao Forest, Sargent A-13 (US), R. A. Howard 12602 (GH), Winters 2213 (A).

Lindau described *Coccoloba urbaniana*, citing four collections, two by Crueger (2694 & 2692) from Trinidad and two by Sintenis (1527 & 1585) from Puerto Rico. His description, however, is obviously based on the material from Puerto Rico. No holotype was selected at the time. In his second publication of monographic studies on the genus *Coccoloba* in the Symbolae Antillanae, Lindau lists and keys *Coccoloba urbaniana*, but cites only the Sintenis collections. In fact, the two Crueger collections are not cited anywhere in this publication. It appears that Lindau was, in practice, accepting the species *Coccoloba urbaniana* for Puerto Rico by excluding the Trinidad material.

Britton in 1924 described *Coccoloba borinquensis*, selecting Shafer 3448 as the type specimen. He reports that this collection had been "erroneously included by Lindau in *Coccoloba Urbaniana* Lindau of Trinidad." The Shafer material was collected in 1914 and I can find no indication that Lindau saw the type specimen at the New York Botanical Garden or any duplicates or fragments of this collection. I can only conclude that Britton was referring to a misidentification and that he had overlooked the later Lindau reference which essentially limits the species to Puerto Rico.

Coccoloba borinquensis Britton has been considered endemic to Puerto Rico and has been collected many times, principally in the Luquillo Mountains and the Maricao National Forest. I have studied several populations of this plant in areas similar to mossy forests where it was most abundant. The species as recognized by Britton is a shrub, or rarely a small tree, and is characterized by anomalous and apparently teratological development of the inflorescence axis and the leaves. Both are enormously thickened in living condition and when dried as specimens. In many specimens the rachis thickens as the fruit develops, so that when the fruit falls,

the pedicel is immersed in the fleshy axis tissue and the dried inflorescence axis appears to be deeply pitted. The anomalies in the collections cited are numerous. In collections by Sargent, Wilson and Gregory the axis varies in thickness along its length, being thin, almost tenuous at the base and swollen in the middle and at the apex. Many of the specimens in the collection by Sintenis are thickened and branched at the upper end. One of the specimens collected by Gregory is flattened and obviously fasciated at the apex.

The leaves likewise show variation of an anomalous nature in both living condition and when dried. Many of the leaves seemed almost succulent when fresh, but thick and heavy rather than coriaceous when dry. The veins vary in the degree of prominence in the specimens cited, but such a character is not taxonomically reliable.

Populations of this plant seen in Puerto Rico and the collections on hand show a definite gradation of the characters Britton used to identify this species into the typical form of *Coccoloba swartzii*. However, the conspicuous nature of the abnormality in the field as well as in the herbarium makes it desirable to acknowledge these Puerto Rican populations as forms.

Meisner described with a query a variety of *Coccoloba swartzii* called var. *portoricensis*. Subsequent monographers and workers on the West Indian flora have been unable to place this taxon. Lindau in 1890 studied a drawing of the specimen Meisner cites and thought it might be related to *Coccoloba diversifolia* Jacq. (*C. laurifolia* Lindau) or *Coccoloba swartzii* Meisner (*C. diversifolia* or *C. barbadensis* Lindau). Meisner did not give the name of the collector and as Britton did not recognize *Coccoloba swartzii* Meisner from Puerto Rico, he also was unable to associate the variety Meisner described with any other species. I have seen the Meisner material at the De Candolle Herbarium in Geneva. It was collected by C. G. Bertero in 1820. A portion of this collection appears in the material I have on loan from the Missouri Botanical Garden herbarium. The Bertero material typifying *C. swartzii* var. *portoricensis* is intermediate between the anomalous *C. swartzii* forma *urbaniana* and the typical *C. swartzii*. It is easily matched by material from the Dominican Republic collected near Puerto Plata and specimens from Seibo, by other collections from Puerto Rico and by some from Jamaica. *Coccoloba swartzii* forma *urbaniana* intergrades through material such as *Coccoloba swartzii* var. *portoricensis* into typical material of *C. swartzii*. The transition is so gradual and yet so complete throughout a number of collections that it is impossible to recognize the Meisner variety as a valid taxon.

Coccoloba rugosa Desf. Cat. Hort. Paris, ed. 3, 389. 1829; Weddel, Ann. Sci. Nat. ser. 3, 13: 262. 1849; Meisner, DC. Prodr. 14: 152, 1856; Lindau, Engl. Bot. Jahrb. 13: 203. 1890.

Coccolobis rugosa Brit. & Wils., Sci. Surv. P.R. 5: 269. 1924.

Coccoloba macrophylla Desf. Tabl. 38. 1804, nomen; Desf. ex Hooker, Bot. Mag. 76: t. 4536. 1850.

Coccoloba macrantha Steud. Nom. 1: 390. 1821, nomen.

Shrub or tree to 15 m. tall, trunk to 10 cm. diameter breast height, frequently unbranched or with few very long erect strict branches, these stout, sulcate-angled to almost winged or sharply ridged, glabrous, ochreae 4–7 cm. long, rigid, coriaceous, oblique at the apex, persistent; petioles very short or wanting; leaf blades obovate or rhomboidal when young becoming orbicular to obovate, 25 × 26, 37 × 42 to 60 × 45 cm. long and broad, rigid coriaceous, conspicuously bullate or wrinkled, the margin recurved, glabrous, venation immersed above, prominent below, ultimate nerves conspicuous, blade punctate dotted above, appearing punctate below due to heavy lignification in mesophyll around veins, apex obtuse, base cordate to cordate clasping, the basal lobes often extending 15 cm. below the petiole; inflorescence terminal, 30–45 rarely to 75 cm. long, densely flowered, minutely puberulent, ochreae of inflorescence axis to 4 cm. long, membranaceous above, coriaceous below, slightly puberulent, staminate flowers in clusters of 4 to 18, the pistillate flowers in clusters of 2–6, bracts lanceolate, acute, 1–2 mm. long, puberulent, ochreolae, membranaceous, to 1.5 mm. long, puberulent, pedicels 5–13 mm. long, puberulent, hypanthium 2 mm. long, perianth lobes 1.5 mm. long, ovate, reflexed at maturity of flower, stamens 6–12, usually 8, functional stamens with filaments 2 mm. long, pistil rudiment shorter, sterile stamens 1 mm. long, functional pistil 1.5–2 mm. long, styles 1 mm. long; fruit ovoid, orange red in color, obscurely 3-angled, slightly constricted to a short stipitate base, the apex acute with the achene generally protruding beyond the perianth lobes when mature, mature fruit 5–7 mm. long, 3–5 mm. in diameter, perianth lobes appressed and imbricated, not coronate.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Catano, Britton & Britton 9334 (NY, US), Britton, Britton and Brown 6994 (F, GH, NY, US); Cayey, Sintenis 2171 (GH, US); Humacao, Sintenis 5178 (B, G, GH, MO, S, US); Lago San Jose, Hioram s.n. (NY), Dale s.n. (NY); Martin Peña, Stevenson 1424 (US); Santurce, Heller 1358 (F, NY, US); Sierra de Luquillo, La Estancita, Eggers 827 (B, G, GH), Eggers 655 (C); Sierra de Naguabo, Shafer 3671 (NY, NEOTYPF; US). CULTIVATED SPECIMENS: Hort. Paris (C, G, GH).

Desfontaines in a series of publications listed the species of *Coccoloba* growing under cultivation in the Botanical Gardens in Paris. In one of these lists published in his *Tableau de l'école de botanique du Muséum d'Histoire Naturelle* (Paris), p. 18. 1804, Desfontaines lists the name *Coccoloba macrophylla* but as a nomen nudum without a description. In the second edition of the same work, page 46, 1815, *Coccoloba macrophylla* is not listed and a new name, *Coccoloba rugosa*, is given but without a description. *Coccoloba rugosa* is also listed in the third edition (1829) of the Catalogue and this time validly published with a description on page 389.

Specimens of *Coccoloba rugosa* were widely distributed to other botanical gardens in that period and numerous specimens are found in European herbaria, generally without data other than the name and the notation,

"hort. paris." In Geneva, for example, there are four sheets of this species, two labelled *Coccoloba rheifolia*, one labelled *Coccoloba macrophylla* and one sheet labelled *Coccoloba rugosa* and indented under this name *Coccoloba macrophylla*. W. J. Hooker was unable to find a description of this apparently widely cultivated plant and so in 1850, with John Smith, published a plate illustrating *Coccoloba macrophylla* and a description in the Botanical Magazine (76: *pl. 4536*. 1850). The plant was then under cultivation at Kew and its source was given as Desfontaines. The description and illustration of Hooker and Smith was copied, translated and republished by Lindley and Paxton (Flor. Gard. 1: 191, *f. 94*. 1850-1) and Lemaire (Jard. Fl. 1: *tab. 47*. 1851 and Fl. de Serres 6: 267, *tab. 617*. 1850). Planchon apparently saw the later publication and in Fl. de Serres 7: 160. 1851 referred to an earlier publication of Weddel (Ann. Sc. Nat. 3rd. ser. 13: 262. 1849) which stabilized the nomenclature by placing *Coccoloba macrophylla* in synonymy with *Coccoloba rugosa*.

Hooker makes the suggestion that Desfontaines himself realized the unsuitability of the epithet *macrophylla* for this species and adopted the more appropriate name of *Coccoloba rugosa*. Previous students of this group have failed to indicate a type specimen. Although horticultural material from Paris is available, the specimens seen are either sterile or with immature flowers. Shafer 3671 has been selected as the type number. It is a pistillate plant with mature fruit and this neotype is the specimen in the herbarium of the New York Botanic Garden.

Both Meisner in his treatment of the species for the Prodromus and Lindau in his monograph refer to specimens of this species from St. Thomas. Britton and Wilson report the plant is "not known on St. Thomas at the present time; it may have grown there before the forests were cut away." The specimen from St. Thomas in the Delessert Herbarium was attributed to Ventenat 142. A similar specimen in the Copenhagen Herbarium collected by Ventenat originated in the Vahl Herbarium. The reference of these two specimens to St. Thomas can be seriously questioned. I was unable to locate the species growing in St. Thomas in 1950.

The specimens mentioned above which originated as "hort. paris" bearing the name *Coccoloba rheifolia* raise the question of the correct assignment of this species described by Desfontaines to *Coccoloba latifolia* Lam. as Lindau has done (Engler, Bot. Jahrb. 13: 133. 1890). Certainly the flowering specimens cited bearing the name *C. rheifolia* should be assigned to *C. rugosa*.

Coccoloba rugosa is similar to *C. sintenisii* in having the long pedicels and brightly colored inflorescences. *Coccoloba rugosa* is easily distinguished by the larger sessile and rugose leaves. It is known in Puerto Rico as "ortigon."

Coccoloba pubescens L. Syst. Nat. ed. 10, 1007. 1759; Hooker, Bot. Mag. 59: *t. 3166*. 1832; Fawcett & Rendle, Jour. Bot. 51: 123. 1913.

Scortearia arbor Americana, amplissimis foliis, aversa parte nervis extantibus

hirsutie ferruginea refertis; Plukenet, *Phytographia* t. 222, f. 8. 1691.
Coccoloba rubescens L., Sp. Pl. ed. 2. 523. 1762, lapsus calami.
Coccoloba grandifolia Jacq., Enum. 19. 1760.
Coccolobis grandifolia Brit. & Wils., Sci. Surv. P.R. 5: 269. 1924.
Coccolobis pubescens Sandwith, Jour. Bot. 78: 98. 1940.
Coccolobis antiquensis Sandwith, Jour. Bot. 78: 98. 1940.

Mature tree to 40 feet tall, diameter 12 inches, much branched above; adventitious shoots generally strict and sparsely branched, to 30 feet tall; branches stout, terete, slightly swollen at nodes, strongly grooved or striate; ochreae 2 cm. long, membranaceous and evanescent above, coriaceous and persistent below; petioles stout, 1-2 cm. long, densely tawny pubescent; blades large, generally orbicular, except for terminal leaf, frequently broader than long, 30×40 , 50×80 cm. long and broad, coriaceous, rugose or bullate when mature, thin and plane when young, apex rounded, base rounded to cordate, the basal lobes commonly encircling the stem, terminal leaflet commonly rhombic, longer than broad when mature, densely tomentose; veins slightly impressed above, all venation conspicuous and reticulate below, midrib and secondary veins persistent pubescent above, the others sparsely pubescent when young becoming glabrate above, margin irregular commonly undulate; mature branches terete, swollen at the nodes, lenticels not conspicuous, tomentose to pilose; ochreae to 1 cm. long, generally completely deciduous, pubescent; mature shoot leaves vary considerably in size and shape, leaves of completely mature plant (as represented by *Howard* 12143, 12352) with petioles 3-6 mm. long, inserted below the ochreae, densely short pubescent, blades broadly orbicular to orbicular-ovate, 7.5×10 , 4×6 cm. grading into size of leaves of adventitious shoot, rugose or bullate; apex rounded, base cordate, the lobes rounded and only rarely approximate, sparsely pubescent above to glabrate, densely or sparsely pubescent below or glabrate, margin undulate, venation of 5 pairs of primary veins, arcuate to the margin, strongly anastomosing, slightly impressed above, conspicuous and reticulate below; inflorescence terminal, often stout, basal ochreae to 7 mm. long, membranaceous, peduncle to 1.5 cm. long, rachis minutely and often densely puberulent, 10-18 cm. long on mature shoots, to 45 cm. long on adventitious shoots, bracts broadly ovate, about 1 mm. long, puberulent, ochreolae membranaceous, spreading, 1 mm. long, minutely puberulent or glabrate; staminate flowers 2-4 per locus, pedicels 2-3 mm. long, puberulent, perianth lobes broadly orbicular 1.5 mm. long, 2 mm. wide, puberulent outside, hypanthium 0.5-1 mm. long, filaments 2 mm. long, anthers 0.5 mm. long, pistillate rudiments glabrous, 0.5-1.5 mm. long; pistillate flowers 2-3 at a locus, 2-3 mm. long, hypanthium to 1 mm. long, puberulent, perianth lobes orbicular 1-1.5 mm. long and wide, puberulent outside; stamens rudimentary, 0.5-1 mm. long, sterile; pistil glabrous or rarely slightly puberulent 1-2 mm. long, slightly 3-angled, style glabrous, 1-1.5 mm. long, stigmas flattened or slightly bilobed; fruit globose to ovoid, 5-6 mm. long and 4-5 mm. in diameter, fruiting perianth imbricate at apex, not turbinated, hypan-

thium with conspicuous vascular bundles, achene sub-globose, dark brown, shining, slightly tri-radiate at the apex, fruiting pedicels puberulent, 3-4 mm. long.

DISTRIBUTION: Hispaniola, Puerto Rico, Barbuda, Antigua, Montserrat, Nevis, Guadeloupe, Dominica, Martinique, St. Lucia.

Puerto Rico: Guajataca, *Sargent B-1* (US); La Chiquita near Maricao, *Britton & Cowell 4272* (F, NY, US); Maricao Insular forest, *Howard 12600* (G); Maricao, *Stevens & Hess 3715* (NY); Utuado, *Britton & Cowell 981* (NY, US), *Sintenis 5925* (GH, US). **COMMON NAME:** "Moralon."

Coccoloba pubescens was described by Linnaeus in his *Systema* in 1759 at which time he cited a Plukenet illustration and description. Unfortunately the Plukenet illustration is poor and does not match any of the material I have cited as to leaf shape or the relative length of the petiole. In fact, the illustration shows a leafy branch arising from an ochrea in the position of a petiole or leaf. Fawcett and Rendle (*Jour. Bot.* 51: 123. 1913) reported there was no specimen of this species in the Linnaean Herbarium but that the Plukenet specimen was preserved in the Sloane Herbarium at the British Museum. An examination of this specimen showed it consisted of a terminal and juvenile leaf and bore little relationship either to the drawing of the plant as seen in the field or to the herbarium specimens cited above.

The specific location from which the type specimen originated was presumably Barbados. I have seen and collected the species on islands from St. Lucia to Hispaniola. *Coccoloba pubescens* is also reported from Mexico, Guiana and Brazil, but I have not seen specimens from these areas. Patrick Browne described a plant from Jamaica which was referred to this species by Fawcett & Rendle. Recent collectors have failed to locate the species in the area mentioned by Browne and it must be concluded that Browne's reference applies to adventitious leaves of *Cordia sebestena* (see Howard, *Jour. Arnold Arb.* 38: 105. 1957).

A study of a great number of colonies in the West Indies has indicated that there is a tremendous range of variation in single plants and in colonies of this species. *Coccoloba pubescens* is generally found in drier areas commonly on the windward slopes and generally near the seacoast. The large leaves of the plants appear to be unaffected by salt spray. It has also been found in the mountains and occasionally in more moist wooded areas. Specimens planted in the Maricao National Forest in Puerto Rico, an area of very moist environment, apparently are doing well.

In general appearance in the field, *Coccoloba pubescens* is a conspicuous plant. The habit is wand-like, unbranched except near the top and bearing extremely large leaves. A plant 20 feet tall may be only 1-2 inches in diameter at breast height. These invariably are young saplings of adventitious shoots which are produced when the original trunk is felled. John Beard's illustration of *Coccoloba pubescens* in St. Lucia (as *C. grandifolia* in *The Natural Vegetation of the Windward and Leeward Islands*,

f. 32. 1949) is a good example of such a stand of young trees and adventitious shoots. The wood of even young plants is hard and is valued for charcoal. These plants are cut frequently, which prevents many stands from reaching maturity. Most descriptions of this species have been compiled from a study of herbarium specimens of these young plants or of adventitious shoots.

The only undisturbed mature trees I have seen in the islands from St. Lucia to Jamaica were found in remote and undisturbed areas of Hispaniola. Thus the description given here, while at variance with most published descriptions, is based on a field knowledge of this species and exemplified by personal collections (*Howard 12143* and *12352*) from above Puerto Escondido and from Beata Island in the Dominican Republic. Several of Ekman's collections from within Barahona peninsula agree with this description; e.g., *Ekman H-6947*.

A real problem is encountered in compiling a description of this species. Herbarium material cited in general represents adventitious shoots or young plants. These abnormal specimens with large leaves represent the plant as commonly seen in the field. I now know that the plants may remain in the juvenile leaf condition for as long as twenty-five years. One such specimen is in a fence row of known age in the Dominican Republic. Only one terminal branch of the tree developed the smaller leaves characteristic of the fully mature plant.

Coccoloba pubescens will produce flowers and fruit while bearing juvenile leaves. The inflorescences of such plants may reach 45 cm. (*Howard 11863*) in length and Eggers reports one specimen with a raceme 65 cm. long. This is in contrast to a raceme of 15–18 cm. in a fully mature branch. The flowering or fruiting herbarium specimens will show all the range of size from the largest leaves (50 × 80 cm.) to that reported for fully mature leaves 4 × 6 cm. or 7.5 × 10 cm. (*Howard 12143*). It is difficult to visualize this range of variation unless one has seen it in the field.

The development and amount of pubescence is likewise a variable character. Observations made in the field indicate that the amount of pubescence may be a matter of individual plant variation in a colony. Generally the immature leaves are pubescent and become glabrous except on the veins. However, some large thin young leaves of adventitious shoots were found to be glabrous, while older leaves on the same shoot were pubescent. Generally the leaves of the adventitious shoots bore more pubescence than those of older shoots. Britton and Wilson in describing this species for Puerto Rico and the Virgin Islands offer a complete description that in some aspects appears to be original. It is certainly not taken directly from Lindau's monograph, nor can I find any similarity in the descriptions of more recent students of the West Indies. However, Britton and Wilson's description is not supported by herbarium material of fertile plants. There are in the herbarium of the New York Botanical Gardens two photographs mounted on herbarium sheets, one of a woman holding the large leaf from an adventitious shoot of this plant and

one of a thicket composed of this plant, all of which bear large leaves. It appears to me that Britton must have seen mature plants in the field, although herbarium records and many portions of his published description indicate a knowledge of the large-leaved adventitious shoots only.

I saw many areas on the south coast of Puerto Rico where single or few plants of *Coccoloba pubescens* were present. I did not see a single mature tree with the smaller leaves and the inflorescences and fruit of the older plant. Plants with adventitious shoots and leaves comparable to those photographed and described by Britton (e.g. 1 m. in diameter) were seen only in plantings of this tree in the Maricao National Forest in regions of higher rainfall.

Britton and Wilson report this to be a tree "to 25 m. high," the racemes "densely many-flowered, 4-7 dm. long," characteristics which do not agree with specimens I have seen in the field. The remainder of Britton's description of the vegetative portions applies to the exaggerated, abnormal individual in adventitious shoot condition.

In the second edition of *Species Plantarum* the species name of this binomial was misprinted as *Coccoloba rubescens*.

The epithet *Coccoloba grandifolia* Jacq. published in 1760 is a synonym of *C. pubescens* L. Britton and Wilson and a few other recent authors have accepted Jacquin's name, apparently overlooking the earlier valid publication of *C. pubescens* by Linnaeus.

In 1940 Sandwith described a new species under the name *Coccolobis antiguensis* based on collections by Box 1496 and 301. This species was suggested as allied to *C. pubescens* but differed in the aspect of the leaf. It was further suggested that *C. antiguensis* might represent a hybrid between *C. uvifera* and *C. pubescens*. In 1950 I searched the area around Carr's Gut for the single tree from which Box made the two collections cited by Sandwith. Unfortunately, the tree could not be located and may no longer exist, as the area was heavily cultivated and drastically cut over. In the specimens cited above, all the characters given for *C. antiguensis* can be found. The collection Box 301 is definitely taken from an adventitious shoot. The U. S. National Herbarium specimen of this number (US 1535774) is the typical rhombic terminal leaf of adventitious shoots of *C. pubescens*. Box 1496 is a fertile collection; however the tortuous stems, the pubescence and the flat blades can be found in many other specimens. *Coccoloba antiguensis* is known only from pistillate material. A collection by John Beard and one of my own from the Wallings area of Antigua show the same plane leaves with the veins slight on the lower leaf surface. Beard 283 can be considered a match for Box 1496 in the foliage. Beard's collection is in fruit and the fruits are typical of *C. pubescens*.

***Coccoloba uvifera* L. Syst. Nat. ed. 10, 1007. 1759; Lindau, Engl. Bot. Jahrb. 13: 204. 1890, Symb. Antill. 1: 231. 1899; Fawcett & Rendle, Fl. Jam. 3: 119. 1914.**

Polygonum uvifera L. Sp. Pl. 365. 1753.

Guaiabara uvifera (L.) House, Am. Midl. Nat. 8: 64. 1922.
Coccolobis uvifera Brit. & Wils., Sci. Surv. P.R. 5: 268. 1924.

Tree of strand areas, 2–15 m. tall; branches terete, stout, papillose to pilose, the nodes not tumid; ochreæ rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, puberulent to pilose; petioles stout, 7–10 mm. long, papillose to pilose; leaf blades orbicular to reniform, 6 × 8, 11 × 13, 13 × 18 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the midrib and primary veins prominent on both surfaces, frequently brightly colored when fresh, the primary veins 3–5 pairs, usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, secondary venation minutely reticulate or obscure; apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe often extended around the petiole; leaves of adventitious or fast-growing shoots usually variable in size and shape, but commonly obovate; inflorescence stout, 15–13 cm. long, rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ochreolæ membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the perianth yellow-white or greenish, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long, the fruit obpyriform, 1.2–2 cm. long, 8–10 mm. in diameter, narrowed at the base, rounded-truncate at the apex, the perianth lobes appressed against the apex of the achene, perianth rose-purple when mature, the achene black.

DISTRIBUTION: General along beaches of Florida, Bermuda, the Bahamas through the Caribbean area to South America.

Puerto Rico: Cataño, Millspaugh 178 (F, NY); Condado, Britton, Britton & Brown 7065 (NY); Fajando, Evermann 1243 (US), 1245 (US), Heller 1013 (US); Mayaguez to Guanajubo, Sintenis 765 (GH, US); Ponce, Sargent 568 (US); San Juan, Rose 21607 (US), Sintenis 765b (US); Santurce, Stevenson 343 (US), Heller 1392 (F, NY); Yauco, Underwood & Griggs 719 (F, NY, US). Culebra Island: Millspaugh 1786 (F). Mona Island: Stevens 6339 (NY). Vieques Island: Morrow 143 (US), Shafer 2586 (NY, US). Anagada: Britton & Fred-loch 970 (NY, US). St. Croix: James 8 (GH), Ricksecker 17 (F, MO, NY), Mrs. J. J. Ricksecker 108 (F, MO). St. Thomas: Eggers 216 (GH), 328 (B), Hjalmarsson 17 (S); Kuntze 5586 (NY). Virgin Gorda: Fishlock 333 (NY).

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760, Hist. Stirp. Amer. 114, pl. 76. 1763; Howard, Jour. Arnold Arb. 30: 421. 1949.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. 13: 158. 1890; Urban, Symb. Antill. 1: 227. 1899; Fawcett & Rendle, Flora Jam. 3: 116. 1914 and all recent authors, not Jacquin.

Coccolobis laurifolia Brit. & Wils., Sci. Surv. P.R. 5: 268. 1928, not Jacq.

Coccoloba longifolia Schmidt, Fedde Rep. Sp. Nov. 24: 73. 1927, not Fischer.

Guaiabara laurifolia House, Am. Midl. Nat. 8: 64. 1922 (as *Guaiabara*).

Shrub or small tree to 7 m. tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly tumid; ochreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; petioles 7–10 mm. long, glabrous, leaf blades ovate, oblong, elliptic, lanceolate or obovate, variable on a single shoot, the apex rounded, obtuse, acute or acuminate, the base cuneate to rounded or subcordate, 4 × 3.5, 7 × 5.5, 8 × 4.5, 12 × 8 cm. long and wide, coriaceous, often shining above, dull beneath, glabrous, the midrib and primary veins slightly prominent above, the secondary venation reticulate on both surfaces, the primary veins 3–7 pairs, arcuate, anastomosing before reaching the margin, the margin entire, commonly slightly recurved; leaves of adventitious shoots similar in shape to those of normal growth but larger in size, 17 × 8, 24 × 13, 32 × 12.5 cm. long and wide on petioles 1–2.5 cm. long; leaves of windswept specimens often much smaller than those of normal shoots, 2 × 1.3, 3 × 2 cm. long and wide; inflorescence terminal 4.9, 9, 11 to 18 cm. long; rachis glabrous; staminate flowers in clusters of 2–5, the pistillate flowers solitary; bracts ovate, less than 0.5 mm. long, 1 mm. broad, glabrous; ochreolae membranaceous, less than 0.5 mm. long, glabrous, the flowering pedicels 2–4 mm. long, glabrous; hypanthium 1 mm. long, the perianth lobes 2 × 2, to 3 × 1 mm. long and broad, filaments of functional stamens 1 mm. long, fruiting pedicels 3–4.5 mm. long; fruit globose to obpyriform 10 × 7, 12 × 8, 13 × 8 cm. long and thick, perianth lobes appressed at the apex of the achene.

DISTRIBUTION: Florida and the Bahamas, through the West Indies to South America.

Puerto Rico: Bayamon, Britton & Britton 7944 (NY), Heller 400 (F, NY, US), 4687 (F, GH, MO, NY, US), Johnston 904 (US); Cabo Rojo, Sintenis 714 (GH, S, US), 771 (MO, US), Howard 12604 (GH), 12605 (GH); Coamo Springs, Britton, Britton & Marble 2232 (NY, US), Britton, Britton & Brown 5904 (FM, NY); Guanica, Sintenis 3507 (FM, NY); Luquillo Mts., Holdridge 522 (NY); Guayanilla, Britton & Shafer 1812 (NY, US); Martin Peña, Stevenson 1234 (US), 1859 (NY); Ponce, Heller 6189 (A, F, GH, MO, NY, US); Ponce to Penuelas, Britton & Cowell 1309 (NY, US); Quebradellas, Stevens 1720 (NY); Sardinera to Ubero, Britton, Cowell & Hess 1774 (NY, US); San German, Sargent 446 (US); San Juan, Gerhart & Holdridge 525 (NY); Santurce, Heller 1301 (F, NY, US); Yauco, Gardner s.n. (NY). Mona Island: Stevens 6312 (NY), 6379 (NY), 6380 (NY), 6436 (NY). Vieques Island: Shafer 2795 (NY, US). St. Croix: Kingshill, Eggers s.n. (US).

The proper application of the names *Coccoloba laurifolia* Jacq. and *C. diversifolia* Jacq. was discussed in the first paper of this series in the Journal of the Arnold Arboretum 30: 421. 1949.

Coccoloba sintenisii Urb. ex Lindau, Engl. Bot. Jahrb. 13: 157. 1890.

Coccolobis sintenisii Britton & Wilson, Sci. Surv. P.R. 5: 268. 1924.

Tree 20–30 ft. tall, diameter at breast height 4–12 inches, bark rough, scaly, gray; branches glabrous, lenticels linear; ochreae glabrous, mem-

branaceous and deciduous above, the basal portion coriaceous, persistent, extending 3–4 mm. above the attachment on the adaxial side of the petiole but to 1 mm. on the opposite side, petiole inserted on a conspicuous base, 6 mm. long above the base of the ochreae, petiole 2–4 cm. long, stout, i.e. 5 mm. diameter, its thickness diminishing rapidly in the blade, glabrous; mature leaf blade oval to oblong, 9 × 12, 10 × 16, 13 × 16, to 14 × 19.5 cm. long and broad, thick coriaceous, entire, glabrous on both surfaces, the apex obtusely acuminate to obtuse, often almost apiculate, the base unequally cordate, the midrib and primary veins conspicuous below, primary veins immersed or both primary veins and midrib evident above, the ultimate venation inconspicuous on both surfaces; leaves of adventitious shoots to 18 × 24 cm. long and broad on petioles to 5 cm. long; inflorescences generally terminal on lateral shoots, rarely lateral or terminal on main shoots, 5–15 cm. long, the rachises, pedicels and flowers brightly colored, crimson when fresh and purplish red when dry, basal ochreae membranaceous and deciduous or slightly coriaceous at the base, this portion persistent to 6 mm. long and slightly puberulent, the rachis thick, occasionally flattened, usually striate, glabrous, bracts broadly ovate, less than 0.5 mm. long, ochreolae less than 0.5 mm. long, flowering pedicels 4–5.5 mm. long, glabrous; staminate flowers with hypanthium 1–2 mm. long, the perianth lobes 2–2.5 × 1.5–2 mm. long and broad, the stamens with filaments united at the base to 1 mm., the free portion 1.5–2 mm. long, the pistil rudimentary 1–1.5 mm. long; pistillate flowers borne singly, the perianth lobes 1.5 mm. long, 1–1.3 mm. wide, the rudimentary stamens 8–10, the filaments dilated and united at the base, less than 1 mm. long, the pistil obconical, the ovary 1.5–2 mm. long, the styles 3, equal, 1–1.5 mm. long, the fruiting inflorescences 10–20 cm. long, stout at the base, tapering rapidly, the pedicels in fruit 5–6 mm. long; fruit ovoid, very slightly pedunculate, 4–5 mm. in diameter, the perianth lobes persistent, generally appressed but free, to 3 mm. long, the achene circular in transverse section, the hypanthium not evidently vascularized.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Coamo Springs, *Britton & Britton* 10052 (NY), *Britton, Britton & Brown* 6038 (NY); CCC Camp Susua, *Velez* 1120 (NY); Maricao, *Sintenis* 223 (B — TYPE), *Sargent* 393 (US); Maricao National Forest, *Howard* 12603 (GH); Rio de Maricao, *Britton, Stevens & Hess* 2430 (NY, US), *Britton & Cowell* 4218 (F, NY, US); Sabana Grande, *Sargent* 620 (US).

Coccoloba sintenisii is clearly a distinct species characterized by the long pedicels in both flowering and fruiting condition and by the bright red color of the inflorescence.

Britton applied an herbarium name to the specimens from Coamo Springs. A description had been compiled and was found among Dr. Britton's unpublished manuscripts. Other than the reduced brilliance of color in the inflorescence, I can see no significant difference in these specimens from the type or from the specimens cited above. The material from

Coamo Springs can be included within the definition of *C. sintenisii*. Staminate and pistillate flowers are borne singly in all specimens I have seen, although only one staminate specimen is known.

Coccoloba costata Wr. ex Sauvalle, Fl. Cub. 139. 1868; Lindau, Engl. Bot. Jahrb. 13: 155. 1890, Symb. Antill. 1: 225. 1899; Schmidt, Fedde Repert. Sp. Nov. 27: 105. 1929; Howard, Jour. Arnold Arb. 30: 145. 1949.

Coccolobis costata Brit. & Wils., Sci. Surv. P.R. 5: 270. 1924.

Coccoloba verruculosa Lindau, Engl. Bot. Jahrb. 13: 154. 1890.

Coccoloba rupicola Urb., Symb. Antill. 6: 10. 1909; Brit. & Wils., Sci. Surv. P.R. 5: 270. 1924, as *Coccolobis*.

Coccoloba helwigii Schmidt, Fedde Repert. Sp. Nov. 27: 104. 1929.

Coccoloba samuelssonii Ekm. & Schmidt, Fedde Repert. Sp. Nov. 27: 105. 1929.

Coccoloba sp. Urban, Symb. Antill. 4: 656. 1911.

Small tree of shrubby growth or tree to 10 m. tall; branches stout with a ferruginous to golden pubescence this often persisting only in protected spots or at the apex; ochreae membranaceous 4–6 mm. long, ferruginous puberulent to sub-glabrous; leaf blades generally ovate to elliptic, less commonly suborbicular to obovate-orbicular, the apex obtuse or rounded, the base generally slightly and unequally cordated to narrowly unequally decurrent on the petiole, 2.5×2.5 , 5×5 , 7×5 , 11×8 to 18×12 cm. long and broad, coriaceous, golden shining above, dull brown below, midrib and veins impressed above, prominent below, the primary veins 5–7 pairs, arcuate, anastomosing, the blades sparsely pitted above and below, often showing anomalous peltate or variously shaped resinous stomatal secretions below, these abundant when leaf is young and scattered and few in mature leaves, otherwise glabrous; petioles stout, 8–10 mm. long, slightly puberulent; leaves of adventitious shoots to 35×22 cm. long and broad on petioles to 1.5 cm. long; inflorescence terminal, rachis puberulent, 15–20 cm. long, the staminate flowers in clusters of 2–4, the pistillate flowers solitary, the bracts ovate, 0.5 mm. long, the ochreolae membranaceous, 0.5 mm. long, the flowering pedicels 0.5 mm. long, the hypanthium 0.5 mm. long, the perianth lobes 0.5–1 mm. long and broad, the fertile stamens 1 mm. long; fruiting pedicels to 1.5 mm. long, the fruit globose, to 6 mm. long, 3 mm. thick, the perianth lobes coronate.

DISTRIBUTION: Cuba, Hispaniola, Puerto Rico.

Puerto Rico: Aybonito, *Sintenis* 5934 (GH); Utado at Los Angeles, *Sintenis* 5994 (B — TYPE of *C. rupicola*, GH, NY, US); Larez, *Winters* s.n. (A).

The previous treatment considering *Coccoloba costata* which I published was without the benefit of field study of its related species, *C. samuelssonii*, *C. helwigii* and *C. verruculosa* in Hispaniola and *C. rupicola* of Puerto Rico. Following an examination and study of numerous stands of all but the last of these species in the field, I can only conclude that they represent

races, at most, of a single species. As *Coccoloba costata* is the oldest name available, I am referring five species or previously recognized taxa found in Hispaniola and Puerto Rico to *C. costata* and am extending the range of this group to the Greater Antilles, excluding Jamaica.

Coccoloba costata has been considered for many years an endemic species of Cuba. In 1929 Schmidt referred a single Ekman collection from Haiti to this species at the same time he described *C. samuelssonii* and *C. helwigii*. Only two subsequent collections by Ekman have been so annotated. Schmidt compared *C. costata* with his new *C. samuelssonii* and differentiated between them on the shape of the leaf base and the texture and shine of the leaf surface. These are extremely weak characters in the genus *Coccoloba*, holding true only if the actual type specimens of each species were considered. The variation in *Coccoloba samuelssonii* as represented by Schmidt's determinations of Ekman collections and my own observations in the field are tremendous.

Coccoloba helwigii described by Schmidt was based on *Ekman* 8523, cited as the type, and *Ekman* 4944. Schmidt characterized this new species as having generally suborbicular leaves which are minutely punctate below. On the basis of these two characteristics Schmidt compared it with *C. leoganensis* (his *C. rotundifolia*) and *C. buchii*. The leaf shape is matched in other Ekman specimens such as *Ekman* 4684, referred by Schmidt to *C. costata* forma, *Ekman* 2855, referred to *C. costata*, and *Ekman* 8721, referred to *C. samuelssonii*. As all of these collections show variations on single sheets from leaves suborbicular in shape to leaves ovate-orbicular or even broadly ovate, it is felt that the smaller leaves of the type specimens of *C. helwigii* represent the smaller end of the range of variation in leaf size.

The minute punctations seen and mentioned by Schmidt are excretions from the stomata of the leaf. The chemical nature of the substance has not been determined. However, the material dries into peltate, appressed or stalked artifacts which can be lifted free from the stomata and the leaf with a needle. Similar excretions are found in other specimens of *C. costata* which I have seen, but are more distinctly developed in the Hispaniolan specimens than in the Cuban and Puerto Rican material. The original collections cited for *C. helwigii* are unique in having the excretions in every stomatal opening which gives the entire lower leaf surface the aspect of being dotted in dark brown color. This condition, however, seems characteristic of younger leaves, for some of the older and larger leaves on the type sheet of *C. helwigii* are glabrous or lack these artifacts. The same type of excretion is found on the type specimens of the four species cited here in synonymy.

Lindau described *Coccoloba verruculosa*, basing the species on *Eggers* 1762 from Hispaniola and *Sintenis* 5994 from Puerto Rico. The original description is next to that of *C. costata* in his species order. Using Lindau's key, these two species fall into groups separated by the length of the flowering pedicel. However, the key distinction is not borne out in the

species descriptions. From the published descriptions (Engl. Bot. Jahrb. 13: 154-155. 1890), the major differences cited are those of pubescence and number and length of pedicels. Lindau overlooked the pubescence which is present on *Eggers 1762* and *Sintenis 5994* and which is comparable to that of *C. costata*. The difference in number and length of the flowering pedicels is a sexual character not recognized by Lindau or Schmidt. *Coccocloba verruculosa* is based on a staminate plant and *C. costata* on a pistillate specimen (Wright 1393). *Coccocloba verruculosa* is clearly the same as *C. costata*.

The Sintenis collection 5994 from Puerto Rico has had a turbulent history. Lindau cited it in the original description of *C. verruculosa* although the specimen is poor, being only an old and staminate inflorescence axis. In spite of the condition of the specimen, Urban selected several minor and variable characteristics in the length of the petiole, the shape of the leaf base and the nature of the leaf surface and described *C. rupicola*, citing *Sintenis 5994* as the type and only collection. Britton and Wilson had a fragment of the same sterile material and were only able to append the species to their key to the genus as "species not grouped, known from foliage only." However, in their discussion they state that "Lindau erroneously regarded it as the same as *C. verruculosa* Lindau of Hispaniola." *Coccocloba verruculosa* does not differ from *C. costata* in any significant manner and must be included in the latter species.

A second Sintenis collection from Puerto Rico from Aybonito between Algarrobo and Caribbeanos, *Sintenis 5934*, was included in *Coccocloba costata* by Lindau. This material consists of faster growing shoots and is sterile. Urban (Symb. Ant. 4: 656. 1911) felt it represented some other species and Britton and Wilson repeated the suggestion but cited the collection under *C. costata*, appending it to the list of known species.

The two Sintenis collections 5934 and 5994 were until recently the only material of this species known from Puerto Rico. Britton and his colleagues collected intensively in Puerto Rico but failed to find material which could be referred here. Recently Mr. Harold Winters sent me material which he had collected in July 1956 from the limestone hills north of Larez in Puerto Rico. This collection was of ample material with mature fruit and displayed a considerable range of leaf variation. In all characteristics this recent material substantiates the earlier conclusion of the proper association of the Puerto Rican and Hispaniolan species with *C. costata* of Cuba.

COCCOLOBA IN THE BAHAMA ISLANDS

In their publication The Bahama Flora (New Era Printing Company, 1920), Britton and Millspaugh present a key to the genus *Coccocloba*, recognizing six species in the flora, one of which they described as new. Recent collections have failed to add to this number. Several changes of names are required for the species and the generic description used in The Bahama Flora should be altered to recognize the dioecious, rarely monoe-

cious plants having flowers that are functionally unisexual. The staminate flowers are usually in clusters of 2-5 at each node of the inflorescence axis, while the pistillate flowers are borne singly. The key to the species, however, needs little change.

With the resurgence of interest in the Bahama Islands, both by tourists and botanists, it is hoped that additional collections of the vegetation can be made. Some of the gaps in the distribution of the species cited in this paper are probably nothing more than a lack of collections.

In general, the specimens of all species of *Coccoloba* seen in and from the Bahamas are smaller in size than representatives of the same species from other and adjacent islands of the West Indies. The reduction in size seems complete, from the stature of the plants to the size of the leaves on both normal and adventitious shoots, and is evidenced, as well, in the flowers and fruits. This reduction in size is particularly evident in collections referred to *Coccoloba swartzii*. The xerophytic conditions of the islands in the Bahamas, coupled with the inhospitable substrata of limestone, coral and sand, may naturally stunt the species. It is hoped that some fruits of *C. uvifera*, *C. diversifolia*, *C. swartzii*, *C. tenuifolia* and *C. krugii* which have been sent to several of the Bahama Islands from Jamaica, Cuba and the Dominican Republic may grow and, in a few years, allow comparison with voucher specimens of the parent trees on file in the herbaria of the Arnold Arboretum and the Gray Herbarium.

KEY TO THE SPECIES IN THE BAHAMAS

Flowering and fruiting pedicels 1 mm. or more long, exceeding the ochreolae.

Leaves very large, suborbicular, generally broader than long, 7-20 cm. wide. *C. uvifera*.

Leaves ovate to elliptic, obovate or orbicular, longer than broad.

Primary veins arcuate, anastomosing near the margin.

Leaves coriaceous; racemes stiff erect or spreading; fruit 7-14 mm. long. *C. diversifolia*.

Leaves chartaceous; racemes thin, long and drooping; fruit about 4-6 mm. long. *C. tenuifolia*.

Primary veins free to the margin of the leaves. *C. northropiae*.

Flowering and fruiting pedicels less than 1 mm. long and not exceeding the ochreolae.

Inflorescence longer than the leaves; leaves reticulate veined on both surfaces when dry, turning dark brown or black; fruit dark brown, round in cross section. *C. swartzii*.

Inflorescence shorter than the leaves; ultimate leaf venation inconspicuous above, evident below, leaves drying pale tan or green, petioles often buff-colored; fruit reddish brown, distinctly triangular in section. *C. krugii*.

Coccoloba uvifera L. Syst. Nat. ed. 10, 1007. 1759.

Coccolobis uvifera Britton & Millspaugh, Bahama Flora 116. 1920.

Abaco: Brace 1476 (NY). Acklin's Island: Brace 4514 (F). Andros: A. E.

Wright 269 (F, GH). *Anguilla*: *Wilson* 7960 (F). *Crooked Island*: *Brace* 4681 (F). *Inagua*: *Harshberger* 16 (US), *Nash & Taylor* 1028 (NY), 1055 (F, US), 1226 (NY). *New Providence*: *Dewey* 561 (US), *C. F. Millspaugh* 2101 (F), *Northrop* 80 (A, F, GH). *North Bimini*: *Howard* 10188 (A), 10201 (A), 10216 (A). *Silver Cay*: *Millspaugh* 2455 (F). *Turks Island*: *Nash & Taylor* 3772 (F, US). *Watling's Island*: *Hitchcock* s.n. (F).

A description of the species and complete synonymy is given earlier in this paper. Britton and Millspaugh refer *Coccolobis leoganensis* Jacq. to synonymy here. This is now regarded as a distinct and endemic species of Hispaniola.

***Coccoloba diversifolia* Jacq. Enum. Pl. 19. 1760.**

Coccolobis laurifolia Britton & Millspaugh, The Bahama Flora 117. 1920. *Coccolobis tenuifolia* Northrop, Mem. Torrey Bot. Club 12: 34. 1902, not L. *Coccolobis wrightii* Northrop, Mem. Torrey Bot. Club 12: 34. 1902, not Lindau.

Abaco: Great Cistern, *Brace* 1679 (NY); Old Kerr's Point, *Brace* 2012 (FM). **Acklins Island**: *Brace* 4453 (FM, NY). **Andros**: Deep Creek, *J. I. & A. R. Northrop* 721 (FM, G, NY); Long Bay Cay, *Small & Carter* 8584 (FM, G, NY, US); Crow Hill, Bay Cay, *Small & Carter* 8717 (FM, G, NY, US); Mangrove Cay, *Small & Carter* 8491 (FM, G, NY, US); Nicols Town, *J. I. & A. R. Northrop* 443 (A, G, FM, NY); Calabash Bay, *A. E. Wright* 266 (FM, G, NY); Mangrove Cay, *Brace* 4937 (FM, NY). **Berry Island**: Great Stirrup Cay, *Britton & Millspaugh* 2271 (FM, NY, US). **Cat Island**: *Wilson* 7174 (FM, NY). **Crooked Island**: Landrail Point, *Brace* 4571 (NY, FM), *Hitchcock* s.n. (MO). **Exuma**: Harvest Cay, *Wilson* 7889 (FM, G, NY); Georgetown, *Britton & Millspaugh* 3121 (FM, NY, US), *Britton & Millspaugh* 2776 (FM, NY). **Eleuthera**: Harbour Island, *E. G. Britton* 6382 (FM, NY, US), *J. T. Rothrock* 570 (FM). **Great Ragged Island**: Hog Cay, *Wilson* 7873 (FM, G, MO, NY). **Great Bahama**: *Britton & Millspaugh* 2602 (FM, NY, US). **Green Cay**: *Coker* 238 (NY). **Fortune Island**: *Eggers* 3850 (A, G, US), 3996 (G), *Hitchcock* s.n. (MO). **Inagua**: *Hitchcock* s.n. (FM, MO), *Nash & Taylor* 1056 (FM, NY); Mathewtown, *Nash & Taylor* 880 (FM, NY), 1452 (NY); Balsam Hill, *Nash & Taylor* 1270 (FM, NY). **Little San Salvador**: *Britton & Millspaugh* 5687 (FM, NY). **Long Cay**: *Brace* 4045 (FM, NY). **New Providence**: Hog Island, *Wilson* 8307 (FM, NY), 8315 (FM, NY), *Britton & Brace* 353 (FM, G, NY); Nassau, *Ames* s.n. (A), *Britton* 76 (NY), 86 (NY); Grantstown, *Wilson* 8182 (FM, NY), 8176 (FM, NY); West End Bight, *Millspaugh* 2292 (FM, NY); West Bay St. Road, *Millspaugh* 2164 (FM), 2195 (FM), 2159 (FM), *Hitchcock* s.n. (FM, MO), *Britton & Britton* 115 (NY), *Degener* 18971 (A), 18972 (A, MO), 18973 (A), *Britton & Brace* 476 (F, NY). **North Caicos**: *Wilson* 7709 (F, GH, NY), *Proctor* 9043 (A), 9076 (A). **Rose Island**: *Wilson* 7902 (F, GH, NY), *Britton & Millspaugh* 2128 (F, NY), 2124 (F, NY, US). **South Cat Cay**: *Millspaugh* 2431 (F, NY), 2434 (F, NY). **South Bimini**: *Millspaugh* 2379 (F, NY), 2382 (F, NY), *R. A. & E. S. Howard* 10039 (A), 10040 (A), 10041 (A), 10238 (A), 10247 (A), 10252 (A), 10253 (A). **Watling's Island**: *Wilson* 7249 (F, GH, NY).

A full description of the species and the synonymy were given earlier in this paper.

Coccoloba tenuifolia L. Syst. Nat. ed. 10, 1007. 1759, Amoen. 5: 397. 1760, Sp. Pl. ed. 2, 524. 1762; Fawcett & Rendle, Flora Jam. 3: 119. 1914, Jour. Bot. 51: 124. 1913; Howard, Jour. Arnold Arb. 30: 407. 1949, 38: 93. 1957.

Coccoloba leptostachyoides Lindau, Engl. Bot. Jahrb. 13: 207. 1890.

Coccolobis ? *frutescens*, *foliis subrotundis, fructu minore trigone* Brown, Hist. Jam. 210, t. 14, f. 3. 1756.

Coccoloba excoriata L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Flora Jam. 3: 121. 1914.

Coccolobis bahamensis Britton, Bull. N.Y. Bot. Gard. 4: 116. 1905; Britton & Millspaugh, The Bahama Flora 117. 1920.

Coccolobis obtusifolia Northrop, Mem. Torrey Bot. Club 12: 34. 1902, not Jacq.

Shrub, rarely a small tree 6 to 15 feet tall; branches terete, light brown in color, glabrous or puberulent; ochreae membranaceous above and deciduous, coriaceous and persistent below, puberulent; the leaves characteristically borne on lateral shoots and crowded, the petioles short persistently puberulent, 6-9 mm. long, arising from a conspicuous base above the base of the ochreae, the blades generally elliptic, occasionally obovate, ovate, oblong or sublanceolate, 3.5×2 , 7×4.5 , 8×6 , 9.5×6 to 12×10 cm. long and broad, membranaceous to subcoriaceous, the apex acute, short acuminate or rarely obtuse, the base narrowed and unequally rounded to subcordate, the margin entire to undulate, the blade often conspicuously umbonate in the field; midrib and veins flat or impressed above, prominent beneath, primary veins 4-6 pairs, arcuate, the ultimate venations finely reticulate, glabrous above, finely puberulent below, generally tomentose in the axils of the veins and extending on to the lamina persisting or evident as clear hair bases; adventitious shoots with leaves evenly distributed, petioles 2-5 cm. long, the blades 7×9 to 18×16 cm. long and broad; inflorescence terminal from the lateral leafy shoots, to 8 cm. long, weak and hanging generally strongly curved, the rachis puberulent becoming glabrate; staminate flowers 1-4 at the node, the pistillate flowers usually solitary, the bracts broadly ovate, to 0.5 mm. long, the ochreolae membranaceous, 0.5 mm. long, the pedicels 1 mm. long, the hypanthium 1-1.5 mm. long with apparent basal stalk more conspicuous in the pistillate flower, the perianth lobes 1-1.5 mm. long and broad, the functional stamens 1-1.5 mm. long, the functional pistil 1.5 mm. long; fruiting pedicels 1-1.5 mm. long, the fruit ovoid 5-6 mm. long and 4 mm. in diameter with a short stalk 0.5 mm. long, the perianth lobes appressed, the achene tan in color.

DISTRIBUTION: Bahamas, Cuba and Jamaica.

Andros: Mangrove Cay, Small & Carter 8513 (FM, NY), 8525 (FM, K, NY, US), 8537 (FM, NY), 8509 (FM, NY, K, US), 8511 (FM, K, NY, US); Deep Creek, J. I. & A. R. Northrop 706 (FM, G, K, NY); Long Bay Cay, Small & Carter 8572 (BM, FM, G, NY, K, US); Nicholl's Town, Small & Carter 8938 (NY); Brace 5075 (FM, NY), 5276 (FM, NY), 5235 (FM, NY).

Acklin's Island: *Brace* 4373 (FM, NY). **Caicos:** North Caicos, *C. F. & C. M. Millspaugh* 9137 (FM, NY, US), *Proctor* 9086 (A). **Eleuthera:** Harbour Island, *E. G. Britton* 6376 (FM, NY, US); *Brace* 5429 (FM, NY), 5614 (FM, NY). **Great Exuma:** *Britton & Millspaugh* 2955 (FM, NY). **Inagua:** *Nash & Taylor* 1280 (BM, FM, NY), 1352 (FM, NY—type of *C. bahamensis*). **New Providence:** *Britton & Brace* 647 (FM, G, K, NY, US); *Eggers* 4486 (K, NY). **Watling's Island:** *Wilson* 7244 (FM, K, NY), 7355 (FM, G, K, NY).

***Coccocloba northropiae* Britton**, Bahama Flora 117. 1920 (as *Coccoclobis*), Howard, Jour. Arnold Arb. 30: 411. 1949.

Coccocloba leoganensis var. *parvifolia* Griseb. Cat. Pl. Cub. 61. 1866.

Coccocloba retusa Lindau, Engl. Bot. Jahrb. 13: 150. 1890, in part; Northrop, Mem. Torrey Bot. Club 12: 34. 1902. Not Griseb.

Shrub or small tree to 4 m. tall; branches terete, pilose becoming glabrate, nodes slightly tumid; ochreae membranaceous, 2–3 mm. long, glabrous; leaf blades orbicular to obovate or elliptic, the apex rounded, obtuse or emarginate, the base narrowed, 3 × 2.5, 4 × 3 cm. long and wide, thinly coriaceous, glabrous, turning black on drying, commonly shiny above, dull beneath, the midrib and primary veins equally prominent on both surfaces, the secondary venation reticulate, primary veins 4–6 pairs, straight, diffuse branching and becoming reticulate near the margin, not arcuate and anastomosing, margin entire, flat; petioles 3–5 mm. long, short pilose pubescent; leaves of adventitious shoots variable in shape, 5 × 3, 6 × 4 cm. long and wide, on petioles to 7 mm. long; inflorescence terminal 5–7 cm. long, the rachis puberulent, the female more so than the male, the bracts ovate, less than 0.5 mm. long, the ochreolae membranaceous, less than 0.5 mm. long; male flowers in clusters of 2, the female flowers solitary, the flowering pedicels 0.5–1 mm. long, the hypanthium 1 mm. long, the perianth lobes 1 mm. long and wide, the fertile stamens less than 1 mm. long, the stamens of pistillate flowers rudimentary, less than 0.5 mm. long; fruiting pedicels 1.5 mm. long, the fruit ovoid, to 5 mm. long, 3 mm. thick, the perianth lobes appressed against the apex of the achene.

DISTRIBUTION: Cuba, Bahamas.

Andros: *J. I. & A. R. Northrop* 662 (NY), 705 (A, GH, NY), Mangrove cay near Lisbon Creek, *Small & Carter* 8483 (F, GH, NY, US). **Eleuthera:** Gregory Town, *Coker* 358 (NY). **Great Exuma:** *Britton & Millspaugh* 2982 (F, NY, US). **New Providence:** Nassau, *Curtis s.n.* (NY—holotype).

***Coccocloba swartzii* Meisner**, D.C. Prodr. 14: 159. 1856.

Coccoclobis diversifolia Britton & Millspaugh, The Bahama Flora, 117. 1920; Northrop, Mem. Torrey Bot. Club 12: 34. 1902.

Abaco: *Brace* 1481 (FM, NY), 1697 (NY). **Bimini:** South Bimini, *R. A. & E. S. Howard* 10164 (G). **Caicos:** North Caicos, *Wilson* 7708 (FM, G, NY), 7744 (G, FM, NY); *Proctor* 9060 (A). **Crooked Island:** *Brace* 4658 (FM, MO, NY, US). **Fortune Island:** *Rothrock* 264 (FM, G, NY). **Great Bahama:** *Britton & Millspaugh* 2544 (FM, NY), 2396 (FM, NY). **Inagua:** *Nash & Taylor* 909

(FM, NY), 1009 (NY), 1014 (FM, NY), 1428 (NY). **Little Inagua:** *Wilson* 7769 (FM, G, NY). **Long Island:** *Britton & Millspaugh* 6316 (FM, NY); *Coker* 520 (NY). **New Providence:** *Britton & Brace* 231 (FM, NY), 324 (FM, G, MO, NY, US); *Britton & Millspaugh* 2175 (FM, NY); *Degener* 18970 (A); *Hitchcock s.n.* (MO); *J. I. & A. R. Northrop* 143 (FM, G, NY). **Rose Island:** *Britton & Millspaugh* 2122 (FM, NY, US); *Wilson* 7900 (FM, G, NY).

A complete description of this species and the synonymy was given earlier in this paper. The variations of *C. swartzii* throughout its range was discussed in the second paper of this series (Jour. Arnold Arb. 30: 420. 1949).

***Coccoloba krugii* Lindau, Engl. Bot. Jahrb. 13: 145. 1890.**

Coccolobis krugii Britton & Millspaugh, The Bahama Flora 118. 1920.

Acklin's Island: *Brace* 4387 (FM, NY, US), 4495 (FM, NY); *Eggers* 3960 (B, US). **Cat Island:** The Bight, *Britton & Millspaugh* 5917 (FM, NY); Fort Hine, *Britton & Millspaugh* 5948 (FM, NY); Orange Creek, *Britton & Millspaugh* 5779 (FM, NY); Port Howe, *Hitchcock s.n.* (MO). **Caicos:** Dellis' Cay, *C. F. & C. M. Millspaugh* 9225 (FM, G, NY); South Caicos, *Wilson* 7594 (FM, G, NY); West Caicos, *Wilson* 7754 (FM, G, NY); North Caicos, *Proctor* 8845 (A), 9180 (A). **Crooked Island:** *Brace* 4748 (FM, NY); *Hitchcock s.n.* (FM, MO). **Fortune Island:** *Eggers* 3998 (US), 3801 (US); *Rothrock* 261 (FM, G, NY). **Inagua:** *Nash & Taylor* 968 (FM, NY), 1059 (FM, NY); *Hitchcock s.n.* (MO). **Long Cay:** *Brace* 4040 (FM, NY, US). **New Providence:** *Curtis* 71 (A, G, FM, NY, MO, US); *Britton & Brace* 361 (FM, NY), 363 (FM, NY, US), 864 (FM, NY), 372 (FM, NY), 375 (FM, NY). **Watling's Island:** *Britton & Millspaugh* 6194 (FM, NY); *Coker* 473 (NY); *Wilson* 7215 (FM, G, MO, NY), 7324 (FM, G, MO, NY).

A complete description of this species was given earlier in this paper.

THE POTENTIALITIES AND LIMITATIONS OF WOOD ANATOMY IN THE STUDY OF THE PHYLOGENY AND CLASSIFICATION OF ANGIOSPERMS

I. W. BAILEY

VESSELS

IN OUR RECONNAISSANCE of the tracheary cells of the vascular land plants (Bailey and Tupper, 1918), which led to so many subsequent investigations of evolutionary trends in the xylem of angiosperms, we presented two types of evidence. (1) *Intensive* investigations were made of variations in the size, form and pitting of tracheary cells in different parts of the same plant and in different plants of the same species grown under varying environmental influences. (2) *Extensive* comparative data, obtained from a wide range of randomly selected representatives of the gymnosperms and dicotyledons, were statistically analyzed and tabulated. The latter data, in spite of demonstrated variations within single plants and single species, revealed surprisingly consistent changes in the size, form and pitting of tracheary cells at successive levels in the evolution and specialization of vessels in the dicotyledons as-a-whole.

Similar evolutionary trends in the development and specialization of vessels in the primary xylem of monocotyledons have been demonstrated by Cheadle (1942, 1943a, 1943b, 1944).

At present, the development and specialization of vessels in dicotyledons and monocotyledons provide two of the most, if not the most, comprehensive and reliable evolutionary trends that are preserved in surviving representatives of the angiosperms. It should be recognized in this connection that no longer are there uncertainties regarding the directions in which the evolutionary trends are progressing. This is due to the obvious fact that the structure of geologically ancient land plants negates any possibility of deriving tracheids from vessels. As re-emphasized by Frost (1930a, 1930b, 1931), since vessels clearly evolve by modification of tracheids, the most primitive vessels are composed of members which closely resemble tracheids in size, form and pitting. The most highly specialized vessels are those whose constituent tracheary cells least resemble tracheids.

The most primitive vessels in the metaxylem and secondary xylem of dicotyledons and in the metaxylem of monocotyledons are composed of members which closely resemble thin-walled, scalariformly pitted tracheids. Thus, the vessel-members are long, comparatively slender in relation to their length, and (as viewed in tangential longitudinal sections of the xylem) have gradually tapered, extensively overlapping ends. They are thin-walled and angular in cross-sectional view. They differ from tracheids

at functional maturity solely in the dissolution of pit membranes in a number of the bordered pit pairs in their overlapping ends. In the secondary xylem of dicotyledons, such vessels are more or less uniformly distributed and are infrequently in contact laterally with one another. However, where lateral contacts do occur the intervacular imperforate pitting is scalariform.

The members of the most highly specialized vessels — in contrast to those of the most primitive ones — are short, comparatively broad for their length and tend to be oval or circular in cross-sectional view. They have truncated ends regardless of variations in their diameter. There is a single perforation at each end of the cell. The vessels commonly tend to be more or less extensively aggregated in the secondary xylem, and the intervacular pitting is alternating-multiseriate.

In view of such structural differences as these, it is possible to arrange the vessels of both the dicotyledons and monocotyledons in evolutionary trends of increasing specialization. It is important to bear in mind that this can be accomplished *entirely independently* of the various systems of classifying the taxa of angiosperms, thus avoiding circular arguments based upon assumptions regarding the primitive or specialized character of various representatives of the angiosperms. In other words, primitive vessels are distinguished from specialized ones *solely* upon their own structural differences, and *entirely* without reference to the putative primitiveness of the plants in which they occur.

PARALLEL AND CONVERGENT EVOLUTION IN VESSELS

Comprehensive summations of evidence now indicate that there has been an independent, but parallel, evolution of vessels in dicotyledons and monocotyledons, Bailey (1944), Cheadle (1953). Therefore, if the angiosperms are monophyletic, the monocotyledons must have been derived either from vesselless dicotyledons or from common vesselless ancestors. Furthermore, in both of the principal divisions of the flowering plants, as in *Selaginella* and *Pteridium*, vessels evolved by modification of scalariformly pitted tracheids, in striking contrast to the Gnetales where vessels evolved from tracheids having circular bordered pits with conspicuous tori. Thus, available evidence negates any possibility of deriving the angiosperms from the Gnetales, Coniferales, Taxales or Ginkgoales. The similarity between the highly specialized vessels of *Gnetum* and of certain dicotyledons is owing to convergent, rather than parallel, evolution.

The wide range of variability in the reproductive organs of vesselless dicotyledons suggests that vessels may have originated more than once in primitive representatives of the dicotyledons. In addition, much evidence is now available which demonstrates that similar trends of specialization of vessels have occurred independently in many families of the dicotyledons. In other words, similarities due to parallel evolution are surprisingly common in the xylem of dicotyledons.

CORRELATIONS BETWEEN VESSELS, CAMBIAL INITIALS IMPERFORATE TRACHEARY CELLS, WOOD PARENCHYMA AND RAYS

In the case of the secondary xylem of dicotyledons, it is possible by statistical correlations to show that during the evolution and specialization of vessels there are concomitant changes in the fusiform initials of the cambium, Bailey (1920a, 1923), and also in the ground mass of imperforate tracheids which tend to assume an increasingly fiber-like form, Bailey and Tupper (1918), Bailey (1936). In addition, it is possible by statistical correlations to obtain significant clues regarding primitive forms of wood parenchyma (Kribs 1937) and wood rays (Kribs 1935, Barghoorn 1940, 1941a, 1941b), and to study a number of their salient trends of specialization.

CAMBIAL INITIALS

As in the case of vesselless dicotyledons and gymnosperms, the most primitive kinds of vessel-bearing secondary xylem are formed by a cambium having long fusiform initials with gradually tapered, extensively overlapping ends as seen in tangential sections. The anticlinal divisions of these initials are pseudo-transverse, and the resulting cells elongate extensively before they in turn divide anticlinally. Thus, there is a wide range of variability in the length of neighboring initials. Since the frequency of anticlinal divisions and the amount of apical elongation are not constant, the average or mean length of the fusiform initials varies markedly in different parts of a fully matured plant. The most significant of these variations is the increase in mean size during the lateral enlargement of stems, due largely to an increase in mean length of the fusiform initials, but also to a less conspicuous increase in their tangential diameter. Important also are reductions in length of initials at nodes as contrasted with internodes of young stems, at the junctions of large stems with branches or roots, and in burly tissues due to injuries or other abnormalities. Furthermore, dwarfing due to extremely retarded growth in unfavorable habitats reduces the mean size more or less markedly. One should bear in mind in this connection that the fusiform initials continue to divide periclinally, thus forming tracheary derivatives, during their intervals of elongation between successive anticlinal divisions. Therefore, since vessel members elongate slightly, if at all, during tissue differentiation, their variations in length closely parallel the variations in length of the cambial initials.

Secondary xylem containing the most highly specialized vessels is formed by a cambium having short initials with abruptly tapered ends and slight overlap. The anticlinal divisions are radial longitudinal and, owing to the elimination of apical elongation between such divisions, the neighboring initials are of relatively uniform length and exhibit a stratified or storied arrangement in surface view of the cambium. The mean length of the

initials varies somewhat in different parts of a fully matured plant and in plants grown under different environmental influences, but the variations are slight in comparison with those that occur in primitive cambia of dicotyledons and gymnosperms. For example, in different parts of a vesselless tree (*Pseudotsuga menziesii*) selected for comparison, the mean lengths of the fusiform initials varied between 900 μ and 6000 μ , the shortest initial being 280 μ and the longest 8600 μ . In contrast to this, the mean lengths of the initials in different parts of a tree having a storied cambium (*Robinia pseudoacacia*) varied between 150 μ and 190 μ , the shortest initial having a length of 70 μ and the longest one a length of 320 μ .

As in the case of primitive vessels, the mean length of the members of highly specialized vessels closely approximates the mean length of the cambial initials. However, the girth of the vessel members presents an entirely different problem. In primitively vesselless forms of secondary xylem, the tangential diameter of the tracheids is determined by the tangential diameter of the fusiform initials, whereas the radial dimension is due largely to radial expansion during tissue differentiation. It is for this reason that the tracheids exhibit radial seriations in cross sections of the secondary xylem, except in certain cases where the seriations are disturbed by excessive intrusive elongation of the tracheids during tissue differentiation. Furthermore, as the tangential diameter of the fusiform initials tends to increase as a stem enlarges in circumference (Bailey, 1920b), the tracheids of the later-formed xylem tend to be correspondingly broader, as well as much longer, than they are in the first-formed secondary xylem. On the contrary, the girth of vessels is determined by both tangential and radial expansion during tissue differentiation. Where the vessel members are much broader than tracheids, as they so commonly are in highly specialized vessels, they afford no reliable clue regarding the tangential diameter of the cambial initials. It should be noted in passing that the girth of highly specialized vessels varies widely, not only in different taxa and in plants grown under different environmental conditions, but also in different parts of the same plant. The vessels of the later-formed secondary xylem commonly tend to be conspicuously broader than those of the first-formed secondary xylem (Bailey and Howard, 1941). However, such variations in girth are due largely to variations in the amount of lateral expansion during tissue differentiation rather than to differences in the diameters of cambial initials.

IMPERFORATE TRACHEARY CELLS

During the evolution of the taller vascular land plants, there has been a constant necessity of maintaining an equilibrium between rates of conductions and strength in stems (Bailey, 1953). Among vesselless gymnosperms, there is at times a more or less obvious tendency to form tracheids which vary in strength and in their permeability to ascending sap, certain of the

vertically contiguous tracheids being broader, thinner-walled and more profusely pitted, whereas others are more slender, thicker-walled and have a reduced number of relatively small, circular bordered pits. This tendency toward "division of labor" in conduction and strength is most obvious and sharply defined in gymnosperms having pronounced growth rings in their secondary xylem, viz. layers of relatively weak, highly permeable tracheary tissue alternating with dense much stronger ones.

In certain of the vesselless dicotyledons, as in certain of the Bennettitales (*sensu lato*), which do not have a conspicuously zonate secondary xylem, the broader, thinner-walled tracheids tend to have abundant scalariform pitting and to be more or less randomly or irregularly distributed throughout the groundmass of secondary xylem. On the contrary, in the vesselless dicotyledons, *Tetracentron* and *Trochodendron*, as in certain remarkable representatives of the Bennettitales (*sensu lato*) recently described by Hsii and Bose (1952) and Bose (1953), which have conspicuous growth layers, the broad, thin-walled tracheids of the early-wood have profuse scalariform pitting, whereas the slender, thick-walled tracheids of the late-wood are provided with a few, small, circular, bordered pits only.

If the vessels of dicotyledons were derived from scalariformly pitted tracheids in zonal arrangement, it might be anticipated that the most primitive vessels in the secondary xylem would be aggregated in concentric zones. This obviously is not the case, and indicates that they developed by modification of scalariformly pitted tracheids that were loosely diffused throughout the groundmass of thick-walled, mechanically stronger tracheids.

The division of labor between strength and conduction in tracheary cells becomes increasingly intensified during the evolution and specialization of vessels in the secondary xylem of the dicotyledons. As revealed by significant statistical correlations in the dicotyledons as-a-whole, the imperforate tracheids become increasingly fiber-like at successive levels in the evolutionary specialization of vessels and cambial initials, due to proportionally greater elongation during tissue differentiation and to reduction and elimination of borders about the pits.

Even during the earlier stages of the evolution of vessels, there is a tendency for enhanced elongation of the thick-walled tracheids during tissue differentiation, but it is not sufficient to compensate for the marked reduction in length of the cambial initials, i.e. when comparisons are made with vesselless dicotyledons and gymnosperms. As the specialization of vessels progresses, the elongation of the imperforate tracheary cells tends to become proportionally greater until elongations of several hundred percent are not infrequently attained. However, the enhanced elongation does not neutralize the shortening effect of excessive reduction in length of the cambial initials. Thus, the imperforate tracheary cells tend, in general, to become shorter as vessels attain successive levels of increasing evolutionary specialization.

WOOD PARENCHYMA

Wood parenchyma strands ordinarily do not elongate or enlarge their tangential diameter appreciably during tissue differentiation. Since their length and tangential diameter is determined largely by the cambial initials, their size and the size and number of their constituent cells decreases concomitantly with the reduction in size of cambial initials. It should be noted in this connection that, particularly in the case of highly specialized tracheary tissue, the wood parenchyma strands provide reliable clues regarding the dimensions of cambial initials. Furthermore, when they occur in extensive aggregations, they provide a means of determining whether the cambium is of a storied or non-storied type.

The distribution of wood parenchyma in vesselless dicotyledons varies between absent, scanty diffuse, diffuse-in-aggregates and narrow tangentially banded. It is not possible at present to determine with certainty whether absence of wood parenchyma in vesselless dicotyledons is a primitive or a derived condition. However, collateral evidence indicates that the tangentially banded parenchyma of *Pseudowintera* is derived by a modification of the diffuse pattern.

Among woods having primitive vessels, nearly 90 percent have diffuse parenchyma, commonly of the diffuse-in-aggregates type. Absence of wood parenchyma may approximate 10 percent, whereas narrow, tangentially banded apotracheal and scanty paratracheal types are of rare occurrence. Broad-banded apotracheal and abundant paratracheal forms of distribution occur in woods whose vessels have attained relatively high levels of evolutionary specialization. Various mixtures of apotracheal and paratracheal patterns are produced in association with transitional and highly specialized forms of vessels.

Although available statistical data (Kribs, 1937), demonstrate that the various forms of aggregated, apotracheal and paratracheal parenchyma are derived from a primitive, diffuse, apotracheal distribution, they do not provide a thoroughly reliable basis for arranging the diversified patterns in a single linear series of increasing structural specialization. Summations of morphological evidence from various taxa of the dicotyledons now indicate that reductions in the amount of wood parenchyma to terminal, scanty paratracheal, or absent occur independently at various levels of the evolutionary specialization of vessels. Uncertainties exist, however, in dealing with various mixtures of apotracheal and paratracheal parenchyma which may have developed in more than one way. For example, broad-banded apotracheal may have given rise to banded with included vessels, to aliform paratracheal to abundant vasicentric, or vasicentric paratracheal may have led to aliform to tangentially confluent, or both kinds of specialization may have occurred independently in different taxa. Such uncertainties cannot be clarified until more detailed and comprehensive studies have been made of a number of the larger families of the dicotyledons.

WOOD RAYS

Since the rays in secondary xylem are formed by ray initials of the cambium, their dimensions ordinarily are not directly influenced by those of the fusiform initials which form tracheary cells and wood parenchyma strands. However, owing to the fact that new ray initials are periodically formed by division of fusiform initials, there are at times indirect effects that should not be overlooked, particularly in the case of storied cambia.

The ray initials of vesselless dicotyledons and of dicotyledons having primitive forms of vessels are of two distinctly different shapes and aggregations. As viewed in tangential longitudinal sections, there are (1) erect ray initials in vertically uniserial arrangement and (2) more nearly isodiametric ones in multiseriate aggregation. The multiseriate aggregations terminate both upward and downward in uniserial extensions of erect initials. Two types of wood rays are formed by these initials, (1) high-celled uniserial rays, and (2) multiseriate rays whose constituent cells are vertically short in comparison with those of the uniserial rays except in their high-celled uniserial extensions. These extensions appear to be uniserial rays that are attached to the upper and lower margins of the multiseriate rays.

During the evolutionary specialization of vessels, divergent modifications of this primitive form of ray structure occur. Some of the more significant changes involve (a) reduction and elimination of multiseriate rays, (b) reduction and elimination of uniserial rays, (c) reduction and elimination of all rays, (d) reduction in the height of ray cells with concomitant increase in their radial expansion during tissue differentiation, leading to the formation of so-called homogeneous rays, viz. composed throughout of more or less conspicuously "procumbent" cells, (e) excessive reductions or amplifications in the width of multiseriate rays, and (f) arrangement of low rays in transverse stratification where the secondary xylem is formed by a storied cambium.

Although transitional stages in the attainment of the end-products of each of these trends of specialization can be arranged in evolutionary series, the different trends of specialization cannot be combined in a single linear series which closely parallels that of the evolutionary specialization of vessels. Each trend of specialization, with the exception of storied rays, may occur at different levels of the increasing specialization of vessels.

THE ROLE OF WOOD ANATOMY IN TAXONOMY

Recognizing that the salient trends of evolutionary specialization in the xylem have been revealed by statistical analyses of the dicotyledons *as-a-whole*, the question arises, how and to what extent may they be utilized in studying relationships within orders, families, genera and species.

It is no longer justifiable to assume, as has so frequently been done in the past, that one organ or part of a plant is inherently more conservative and

reliable than are all others. From the point of view of the dicotyledons *as-a-whole*, it is evident that each organ or part may be relatively uniform morphologically in certain taxa whereas it is highly variable in others. Furthermore, the rates of evolutionary modification in different parts frequently are not closely synchronized. Thus, any particular evolutionary trend, however reliably established, applies to a single part of the plant *only* and does not *by itself*, provide a reliable basis for classifying the plants from which the evidence was obtained in a similar phylogenetic sequence, since evidence from other parts of the plant may negate such an arrangement. If a truly natural classification of dicotyledons is to be attained, it must be based upon harmonizing evidence from all organs and parts of the plants. It is in this synthesizing task that wood anatomy has a significant role in taxonomy.

There has been, and still exists, a tendency among those who concentrate their attention largely upon the study of wood anatomy to base conclusions regarding relationships and classification solely upon similarities and differences in the structure of the xylem. Such conclusions are unreliable unless supported by the totality of evidence from other parts of the plants. This is owing to the fact that similarities in the xylem, which may be due to parallel evolution, are not necessarily indicative of close genetic relationship of plants unless supported by strong corroborative evidence. Nor are conspicuous differences in the xylem necessarily indicative in all cases of remote relationship, since the evolutionary modification of the xylem may be accelerated in plants where a totality of evidence from all organs and parts is indicative of relatively close relationship.

Thus far, the evolutionary trends in the cambium and xylem of dicotyledons, when considered by themselves, have been most reliable and significant in *negations*. This is owing to the fact that plants which have retained primitive cambia and xylem cannot be derived from plants which have attained uniformly high levels of structural specialization. For example, the monocotyledons cannot be derived from the Ranunculaceae or Piperaceae. Within the dicotyledons, herbs, vines, lianas, succulents and many extreme xerophytes have attained high levels of tracheary specializations and cannot have given rise to trees and shrubs which retain relatively primitive forms of xylem. The relatively highly specialized xylem of the Amentiferae negates any possibility of considering them the primitive stock from which other dicotyledons have been derived.

There are certain details of the trends of specialization in the xylem which need to be more clearly and generally understood in shifting from a consideration of the dicotyledons *as-a-whole* to investigations of the taxonomy of individual taxa of restricted size. In revealing salient trends of evolutionary specialization by analyses of data obtained from the dicotyledons *as-a-whole*, variations due to obtaining specimens from different parts of the plant, from plants of different growth rates, from genetically differ-

ent taxa, etc., tend to neutralize one another. In addition, various localized, divergent trends of specialization do not obscure or confuse the major trends of evolution in the dicotyledons *as-a-whole*. However, when one becomes concerned with taxa of decreasing size, viz. families, subfamilies, tribes, genera and species, such variations and deviations become increasingly significant.

DEVIATIONS IN THE SYNCHRONIZATION OF STRUCTURAL CHANGES IN TRACHEARY CELLS

When *averaged* data are obtained from the dicotyledons *as-a-whole*, the successive evolutionary modifications of the cambium and of the length, form and pitting of its tracheary derivatives tend *in general* to be relatively closely synchronized in passing from the most primitive to the most specialized conditions. It should be kept in mind in this connection, however, that changes in the form, perforations and imperforate intervacular pitting of vessel members tend to be retarded in the metaxylem and first-formed secondary xylem (Bailey, 1944), as also not infrequently in the vessels of smaller diameter in the later-formed secondary xylem. Furthermore, there are families and genera in which one or another of the generally coordinated changes is accelerated or retarded in relation to the others. For example, accelerations in the transformation of scalariform to simple perforations, coupled with retardation in the lateral enlargement of vessels, may at times lead to the formation of relatively long vessel members with steeply inclined, rather than transversely oriented, simple perforation plates. Conversely, excessive enlargement of vessels, coupled with retarded changes in the perforations, may result in broad vessel members with nearly transversely oriented scalariform perforation plates. Precocious enlargement of vessels in vines and lianas, with concomitant changes in perforations and intervacular pitting, results at times in vessel members that are excessively long for their general level of morphological specialization. Conversely, extreme dwarfing, coupled with retardation of changes in perforations and intervacular pitting, frequently leads to the formation of vessel members that are short for their general level of primitive morphological structures. The changes in perforations and in intervacular pitting may be retarded or accelerated in relation to one another, as may those that occur in vessels as contrasted with imperforate tracheary cells.

In view of the occurrence of such localized variations as these, it is evident that considerable caution must be exercised in attempting to arrange the tracheary tissues of the species of a given genus or the genera of a particular family in linear evolutionary series which provide reliable evidence in discussions of relationships, particularly in taxa whose representatives fall within a relatively narrow range of the evolutionary specialization of vessels, e.g. Compositae, Leguminosae, etc. In the case of such taxa, undue emphasis should not be placed upon differences in the dimensions of tracheary cells, in the inclination of perforations, or in the character of inter-

vascular pitting in *randomly collected samples* of various species and genera. Detailed and laborious consideration must be given to the ranges of variability within each plant and within each species if comparable statistical averages are to be obtained.

LOCALIZED DIVERGENT TRENDS OF SPECIALIZATION

It is evident that in dealing with wood rays and with patterns of wood parenchyma distribution one is concerned with a number of divergent trends of specialization rather than with single unidirectional series of increasing evolutionary modification. Each of these trends of modification may occur independently at different levels of the structural specialization of vessels. In other words, parallel evolutionary changes in wood rays and wood parenchyma occur independently in many taxa of the dicotyledons.

Although the major trend of specialization in fusiform initials and in their tracheary derivatives is unidirectional, there are various localized divergent specializations which merit careful consideration in the discussion of taxonomic problems. For example, the tendency to form "tertiary" helical thickenings in tracheary cells is a divergent trend of specialization that has occurred independently in gymnosperms as well as in many taxa of the dicotyledons. Their presence in vessels is not indicative necessarily of close genetic relationship. Nor can it be assumed that such vessels are derived from tracheids with helical thickenings. Another common divergent trend of specialization is the tendency of imperforate tracheary cells to retain their living contents which divide forming septa internal to the lignified secondary wall. Such septate fiber-tracheids and libriform fibers, which function in storage of starch, crystals, etc. as well as mechanically, develop independently at various levels of the evolutionary specialization of vessels. Their occurrence in different taxa is not indicative necessarily of close taxonomic affinities.

Excessive thickening or attenuation of the walls of tracheary cells, unusual enlargement or reduction in the diameter of vessels, and unusually extensive aggregations of vessels in diversified patterns are of not infrequent occurrence in various taxa of the dicotyledons. It is advisable to deal with such structural modifications in terms of localized divergent specializations rather than to endeavor to incorporate them as parts of a single major unidirectional trend of evolutionary specialization. For example, there are taxa whose vessel members have attained relatively high levels of structural specialization as regards their length, form, perforations and pitting, but the vessels are thin-walled and angular in cross-sectional view. *A priori* the latter diagnostic feature might be interpreted as a retention of a primitive structural character. However, summations of evidence in various taxa indicate that there has been a reversionary trend of specialization to a thin-walled angular condition.

The formation of so-called vascular tracheids and vasicentric tracheids similarly represents divergent trends of specialization that occur independently in various taxa. By classical definition, these cells are included

in a broad general category of tracheary elements. However, they do not provide a sound basis for concluding that the evolution of vessels from tracheids is a truly reversible process. This is due to the fact that the end products of these trends of specialization differ markedly from the typical tracheids of vascular land plants in form and in their behavior during tissue differentiation.

CONCLUSIONS

The chief trends of evolutionary specialization in the cambium and xylem of dicotyledons are now so reliably established (except in the case of certain patterns of wood parenchyma distribution) that they can be utilized to advantage in studying salient problems of phylogeny and classification. When considered by themselves, they are most significant in *negations*, since a taxon which retains primitive forms of cambium and xylem cannot be derived directly from a taxon which has attained a uniformly high level of structural specialization. Unfortunately, owing to the frequent occurrence of parallel evolutionary changes, they cannot be utilized in *positive* assertions of relationship or phylogenetic derivation without corroborative evidence from other parts of the plant. However, since evidence from all organs and parts of the plant must be harmonized if a natural classification of plants is to be attained, evidence from wood anatomy should be given due consideration in taxonomy.

It should be emphasized, in conclusion, that the salient trends of evolutionary specialization in the cambium and xylem have been established by statistical analyses of the dicotyledons *as-a-whole*. In obtaining significant statistical averages from large volumes of randomly selected data, the effects of minor variations and localized divergent specializations are minimized. On the contrary, in dealing with the taxonomy of taxa of diminishing size, such variations and localized deviations become increasingly important. More attention should be devoted in the future to much neglected detailed investigations of the ranges of structural variability in individual plants and in individual species and genera. Furthermore, it is essential that anatomical data be obtained from plants of which herbarium vouchers are available.

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STUDIES IN THE BORAGINACEAE, XXIX.
ECHIOCHILON AND RELATED GENERA

IVAN M. JOHNSTON

THE THREE GENERA here discussed, *Megastoma*, *Sericostoma* and *Echiochilon*, include a total of nineteen species endemic in the deserts of northern Africa (Senegal to Somaliland), Arabia, Iran, and Pakistan. Most of these species are rare or very local and subsequent to their original description have been mentioned only briefly and rarely, if at all, in the literature. The many unique or very uncommon features to be observed in the floral structure of these plants have been overlooked or unappreciated.

The relationship of the three genera to the other members of the Boraginoideae is not clear. Although they have features prevailingly suggestive of a relationship among the Lithospermeae, in fruiting structures they are most like the Eritrichieae. Our genera seem to have no obvious direct relations with any of the Old World Boraginoideae. Surprisingly, they seem to be in greatest agreement with *Amblynotopsis* of Mexico and *Antiphytum* of southern Brazil and Uruguay.

Preliminary work on the present report was carried on at the British Museum of Natural History, in the Herbarium at Kew, and in the Herbarium of the Natural History Museum in Paris during a visit to Europe in 1952. Through the kindness of those in charge, I was able to borrow selected specimens from these herbaria for detailed study at the Arnold Arboretum. Subsequently, recently accessioned new collections of *Echiochilon* at Kew and the British Museum have been sent me on loan for identification by Mr. E. Milne-Redhead and Miss Hillcoat. Also of great interest and usefulness has been the loan of the Somali *Echiochilon* from the Botanical Institute, Florence, loaned me by Professor R. E. G. Pichi-Sermolli.

KEY TO THE GENERA

Corolla glabrous inside, minute, shorter than the calyx, throat bearing five obscure weak circular convex invaginations; anthers affixed at or below the middle, becoming dorsiventrally compressed; pollen 3-porate; small annual herbs ranging from the Canary Islands, across North Africa to eastern Arabia. I. *Megastoma*.

Corolla abundantly and conspicuously villose in the throat, throat not at all invaginate; anthers affixed above the middle, becoming strongly compressed laterally; pollen usually 2-colpate but in a few species sometimes also 3-colpate; plants usually fruticose and perennial, only one species annual.

Gynobase plane or even depressed at the center; nutlets with a stout downward directed stipe bearing the attachment at its lower end; stigmas terminal, projecting above the sterile tip of the style; filaments affixed at the summit of the corolla-throat directly beneath the base of the corolla-sinus;

corolla-lobes equalling or even longer than the tubular portion (i.e., tube + throat) of the corolla; calyx deciduous at maturity, the lobes strongly imbricate; cymes usually glomerate, few-flowered; plant of Pakistan and adjacent India. **II. Sericostoma.**

Gynobase elevated, attenuate, usually narrowly pyramidal and more than half the height of the nutlets; stigmas subterminal, always surpassed by the protracted sterile tip of the style; nutlets with a prolonged sessile lateral attachment; filaments affixed deep in the corolla-throat; corolla-lobes shorter than the tubular portion of the corolla; calyx persistent, the lobes valvate or at least not evidently imbricate; corolla small to large, radially symmetric to strongly zygomorphic; inflorescence usually with numerous flowers, usually elongating and becoming unilaterally racemose. **III. Echiochilon.**

I. Megastoma Coss. & Dur. ex Benth. & Hook. Gen. Pl. 2: 851 (1876), in synonymy; Bonnet & Barratte, Ill. Phan. Tunis. t. 11, f. 4-11 (1895), illustration with analysis; Bonnet & Barratte, Cat. Pl. Vasc. Tunis 301 (1896), description; Johnston, Contr. Gray Herb. 73: 64 (1924) and 74: 19 (1925); Brand, Pflanzenr. Heft 97: 77, f. 6 (1931). — Type species: *M. pusillum* Coss. & Dur.

Small annual herb, much branched, erect or becoming decumbent, cinereous with abundant appressed hairs, lowest leaves and branches opposite; leaves all cauline, narrow, abundant; plant fertile nearly throughout and hence developing no sharply delimited inflorescences; flowers produced abundantly along nearly all the leafy stems and branches to form very numerous ill-defined unilateral racemose clusters, the inflorescence never scorpioid; calyx 5-parted, accrescent, base rounded and usually developing a stout pedicel, lobes linear, decidedly unequal (especially in age), connivent in fruit, smallest lobe adaxial, largest lobe one of the two abaxial lobes; corolla white or slightly yellowish or pinkish, minute, shorter than the calyx-lobes, regular, subtubular, completely glabrous or with only a few minute hairs on the outer surface of some corolla-lobes; lobes small, ovate, erect or ascending, rounded at summit; tube (including the throat) cylindric, 3-4 times as long as the lobes; throat not differentiated as to form, inside bearing an ill-defined, circular, low-convex, weak invagination a short distance below each corolla-lobe; annulus not developed; stamens 5, equal, included in the lower half of the corolla-tube; filaments about as long as the anther, arising all at the same elevation very low in the corolla-tube; anther ovate or somewhat cordate, attached at or slightly below the middle, dorsiventrally compressed even after dehiscence, broader than thick and broadest above the base, apex obtuse and sometimes more or less apiculate, base broad and somewhat cordate; thecae distinct but remaining closely juxtaposed below the middle of the anther, their bases rounded or sometimes somewhat apiculate; connective linear, inconspicuous; pollen with 3 coarse circular pores, in polar profile three-sided with the pores forming the truncate corners, ca. 20 μ broad, in lateral profile elliptic ca. 14 μ high and 20 μ broad, the pores equatorial; gynobase elongate, erect,

narrowly pyramidal, 4-angled, from just above the broadened base gradually narrowed to the pointed apex which bears the short style, after the fall of the nutlet the concave sides of the gynobase above the middle commonly bearing a short bristle-like section of the funicle projecting vertically from the broken end of the funicular canal; stigmas terminal, deeply bilobed, lobes subglobose, usually barely surpassing the tips of the nutlets in height; nutlets lance-ovate, usually all four maturing, back convex, base rounded, apex acute, venter with the suture open to form a conspicuous, elongate, narrowly triangular attachment-scar; attachment-scar distinctly lateral, extending from just above the nutlet-base upward almost to the nutlet-apex, 2-2½ times as long as broad, all in a single nearly vertical plane except the broadened lower end which may be slightly oblique and slope somewhat towards the nutlet-base.

Megastoma pusillum Coss. & Dur. in Bonnet & Barratte, Ill. Phan. Tunis. t. 11, f. 4-11 (1895) — Type from "Tunisie méridionale: alluvions de l'Qued Zitoun (Letourn.)."

Small herb, 2-15 cm. tall, usually repeatedly branched, clothed with closely to loosely appressed stiffish straight pale hairs 0.5-1 mm. long; cotyledons frequently persisting even on fruiting plants, blades orbicular, ca. 2 mm. diameter, supported on a very broad short petiolar base which is connate and sheathing below the middle, lower surface of cotyledon glabrous, upper surface hispidulous, the hairs pale and bulbous at the base; leaves numerous, linear or oblanceolate-linear, 5-25 mm. long, 1-2.5 mm. broad, largest ones towards the base of the plant, flat or more or less conduplicate, thickish, veinless, midrib prominent if at all only on the lower surface, both leaf-surfaces bearing appressed stiff hairs arising from thickened bases, apex of blade obtusish or sometimes acute; flowers abundant, borne along most of the leafy stems and forking branches and, in the fruiting state, forming many leafy-bracted unilateral racemes 2-6 cm. long; calyx at anthesis 2-3 mm. long, becoming 4-7(-10) mm. long in fruit, frequently with a pedicel 0.5-1 mm. long; corolla 2-2.5 mm. long, lobes 0.6-0.7 mm. long and nearly as wide, tube about 1 mm. thick, faecal invaginations weak and obscure, 0.2-0.3 mm. diameter, borne about 0.2 mm. below the base of the corolla-lobes; filaments 0.2-0.3 mm. long, arising 0.5-0.7 mm. above the base of the corolla-tube; anthers 0.25-0.3 mm. long, 0.2 mm. broad; gynobase narrow, elongate, 0.1-1.4 mm. tall, ca. 0.5-0.8 mm. broad at the very base; style 0.2-0.3 mm. long; nutlets 1.3-1.8 mm. long, ca. 1 mm. broad above the base, usually sparsely verrucose, with a narrowly triangular lateral scar almost as long as the nutlet-body.

Canary Islands, western Mauritania and southern Morocco eastward, in Algeria, Tunis, Egypt and eastern Arabia, usually in deserts and chiefly in sandy places.

CANARY ISLANDS: Fuerteventura near port of Tarajalejo, sand, April 1912, *O. Burchard* 335 (K). MAURITANIA: Tasiast, Oued Tenebrouret, ca. lat. 21°, long. 15-16°, abundant, Feb. 2, 1937, *Murat* 1946 (G). ALGERIA: El Golia, in

petrosis aridissimis, March 29, 1904, *L. Chevallier* (K); Ghardaia, in aridis glareosis, Feb. 1902, *L. Chevallier* 455 (G); Biskra, sur les collines incultes, May 10, 1853, *B. Balansa* (G). EGYPT: Arabian Desert near Ain Shams to the north of Heliopolis, May 8, 1908, *Emile Burdet* 341 (G); in deserto Belbeys, *Schubert* (K). ARABIA: Kuwait, Airdrome, sandy soil, corolla minute white or pinkish, May and June, 1935, *Dickson* 209 and 253 (K); Bahrain Island, desert at pipeline, Awali wadi, March 13, 1950, *R. Good* 215 (K); Bahrain Island, Jebel Dukhan, March 16, 1950, *R. Good* 216 (K, BM); Jabal Hafit, Oman, April 25, 1948, *W. Thesiger* (BM).

The genus *Megastoma* is notable for its very small subtubular corollas which are shorter than the very unequally lobed calyx. The corolla has very obscure faecal swellings but no differentiated annulus, and is completely glabrous except for a few minute hairs on the outer surface of some of the corolla-lobes. The anthers are short and broad and cordate at the base. The thecae are distinct from the base upward nearly to their middle and almost to the attachment of the anther.

The nutlets and gynobase are beautifully illustrated by Bonnet & Barratte, the swellings in the corolla-throat, which they failed to notice, are shown somewhat diagrammatically in the figure given by Brand. Both Bonnet & Barratte and Brand incorrectly illustrated and described the stigmas of *Megastoma* as simple and capitellate. Actually the stigma is bilobed and frequently almost completely divided. Under high magnification it usually appears to consist of two closely juxtaposed subglobose stigmas terminal on the style.

II. **Sericostoma** Stocks ex Wight, *Icones Pl. Ind. Orient.* 4²: 15, t. 1377 (1848). — Type species: *S. pauciflorum* Stocks ex Wight.

A low spreading shrub with numerous slender much-branched stems, strigose, cinereous; leaves oblanceolate, oblong, or lanceolate, usually acute, thickish, loosely conduplicate, veinless, midrib evident if at all only on lower surface, lowest leaves on the shoot opposite; inflorescence terminal on the branches and branchlets, 3–6-flowered, at first glomerate but eventually short-racemose, bracts 1–2; calyx 5-fid, base thickened and elongate in age and eventually disarticulating; lobes imbricate, lanceolate, acute, subequal; corolla radially symmetric, white, minutely villulose on the surface of some of the corolla-lobes but otherwise glabrous outside, inside abundantly white villose in the throat; lobes as long as the corolla-tube or slightly longer, oblong, minutely lacerate near apex, spreading or recurving; tube (including the undifferentiated throat) stout, weakly ampliate; stamens almost completely exserted; filaments subulate, equal, about as long as the anther, affixed at the top of the throat directly beneath the sinus, anther narrowly oblong, erect, affixed above the middle, with rounded ends, in age with thecae explanate and back to back with the pallid inner surfaces parallel and facing laterally in opposite directions, the dehisced anthers accordingly appearing to be very strongly compressed laterally; connective very narrow and inconspicuous; pollen bicolpate,

usually more or less bilaterally symmetric, 19–23 μ high, 21–24 μ broad, polar profile elliptic, lateral profile quadrate to transversely rectangular; gynobase not elevated, a cartilaginous disk, plane or somewhat depressed at the center, scarred by large circular excavations after the fall of the nutlets; style arising directly from the center of the discoid gynobase, shorter than the nutlets; stigmas 2, as long or longer than broad, vesicular, pallid, swollen, terminal, separated across the apex of the style by a narrow band of sterile stylar tissue but the two stigmas always evidently projecting above it; nutlets 1–4, usually only one maturing, ovoid, abundantly verrucose and tumulose, gray, reddish or brownish, ascending, supported on a short stout vertical laterally affixed stipe; axial edge of nutlet obtusely angulate, straight and vertical or nearly so, formed above the middle by the short low ventral keel on the nutlet-body and below the middle by the ventral side of the stipe, traversed from apex of nutlet to base of stipe by the closed and completely fused ventral suture; seminiferous body of the nutlet ovoid, inclined at an angle of about 60°, its pointed apex held high above nutlet-attachment and its rounded base held directly abaxial to the attachment; stipe stout, solid, smooth on sides, bearing the convex attachment-scar on its horizontal lower end, attached to the body of the nutlet on the sloping underside of the latter just below its middle; funicular canal ascending vertically inside the stipe and entering the seminiferous body of the nutlet just below the middle on the ventral side; seed compressed ovoid with a short radicle, the funicle attached half way up the ventral side of the seed.

A monotypic genus known from Pakistan and adjoining western India.

Sericostoma pauciflora Stocks ex Wight, Icones Pl. Ind. Orient. 4²: 15, t. 1377 (1848); Hooker, Icones 9: t. 804 (1852) — Type from Baikur near Deesa, Scinde, Stocks.

Sericostoma parviflorum Stocks ex Walp. Annal. 3: 135 (1852), lapsus calami.

Stems numerous, 1–5 dm. long; old stems woody, with rough dark bark, 1 cm. or more thick; leaf-bearing branches 1–2 dm. long, 1–2.5 mm. thick, bearing straight, closely appressed hairs 0.2–0.6 mm. long; leaves all cauline, numerous, 5–35 mm. long, 2–10 mm. broad, strigose on both surfaces (hairs closely appressed 0.2–0.6 mm. long, most of them arising from discoid, mineralized bases), lowest leaves on the shoot and branches always forming 1–2 opposite pairs; cymes not scorpioid, usually about 4-flowered, at first glomerate and ca. 5 mm. in diameter, in age more loosely flowered on an axis 5–12 mm. long; bracts 1–2, inconspicuous, 1–3 mm. long; calyx strigose outside, inner surface glabrous, at anthesis 2.5–3 mm. long, with a short broad base, subsessile, lobes 0.7–1.2 mm. long; calyx at maturity having weakly accrescent lobes but an enlarged base, tending to become nutant and at extreme maturity to disarticulate from the inflorescence and to fall away with the nutlet still embraced by the connivent lobes, calyx-base thickened, angulate, elongate and frequently more or less pedicellate; corolla rotate, usually about 5 mm. diameter; lobes 1.5–2 mm. long, 1–1.7

mm. broad, usually with conspicuous dichotomous veins; tube 1.2–1.8 mm. long, 0.8–1.2 mm. thick, gradually but weakly ampliate from the base upward, upper half of tube (i.e. the throat) densely and conspicuously white-villous inside, below the middle of the tube glabrous inside except for a narrow inconspicuous villulose band (marking the site of the undeveloped annulus) ca. 0.2 mm. above the corolla-base; filaments 0.8–1 mm. long; anthers 0.8–1 mm. long, erect; gynobase ca. 1 mm. broad at anthesis, becoming 1.5–2 mm. broad when maturing all four nutlets, scar left by the detached nutlet a shallow excavation ca. 0.5 mm. diameter; style 1–1.3 mm. long, sterile apex surpassed by at least one-fourth of the length of the stigmas; nutlets 2–2.4 mm. long, ca. 1.5 mm. broad, ovoid, usually somewhat lustrous, with a rounded base, a convex dorsum and a broadly acute apex, body of nutlet supported on the sloping ventral under side by a stout vertical stipe 0.5 mm. long and almost 0.5 mm. in diameter; attachment-scar of nutlet on the base of the stipe, rough, convex, situated in the same horizontal plane as the base of the nutlet-body and adjacent to the latter and adaxial to it.

Dunes and other sandy places, chiefly in desert areas and along the coast, in southern Pakistan and in adjacent westernmost India.

SPECIMENS STUDIED: Scinde, *Stocks* in *Hook. & Thomson, Herb. Ind. Orient.* (G); Southeast Punjab, 1886, *J. R. Drummond* 25988 (K); Punjab, *J. R. Drummond* 25987 (K); Baikur near Deesa, *J. E. Stocks* 61 (K); coast of Kathiawar, plentiful low-spreading shrub, *Dalzell* (K); Nargol, open formations in sand along sea, Feb. 24, 1912, *H. M. Chibber* (K); without locality, *V. Jacquemont* 59 (G).

As here redefined, *Sericostoma* is reduced to its original species from Pakistan. Plants of Persia, Arabia, and Somalia previously assigned to this genus are now referred to *Echiochilon*. The two genera, although separable by characters of fundamental importance, are close relations, sharing such distinctive features as bicolpate pollen, vesicular stigmatic tissue, villose corolla-throat, and opposite lowermost leaves. In both the anthers are supramedially affixed and have the inner surfaces of the theca pallid, sparsely and very minutely strigose and eventually explanate. Formerly only plants with excessively zygomorphic corollas were referred to *Echiochilon*. Plants with radially symmetric or with only obscurely zygomorphic corollas were referred to *Sericostoma*. The separation of the two genera on this basis, however, can be supported by no other character and is obviously artificial. As now circumscribed, the monotypic genus *Sericostoma* has numerous characters of fundamental importance. Its nutlets are stiped and are borne on a plane, discoid gynobase. The ventral suture on its nutlets is completely closed and the margins fused all the way from the apex of the nutlet-body down to the nutlet-attachment at the base of its stipe. The style arises directly from the center of the discoid gynobase. Its sterile apex is not prolonged upward above the apices of the stigmas. The stigmas are distinct and are as long or longer than broad. They are not laterally prolonged and together do not form a stigmatic band around the

style just beneath its sterile apex. The stamens are borne at the top of the throat directly beneath the base of the corolla-sinus and are almost completely exserted. The calyx has obviously imbricate lobes and eventually is deciduous while still embracing the mature fruit.

III. *Echiochilon* Desf. *Fl. Atlant.* 1: 166, *t. 47* (1798). — Type species: *E. fruticosum* Desf.

Chilochium Raf. *Ann. Gen. Sci. Phys.* 8: 269 (1821). — A proposed substitute name for *Echiochilon* Desf. (1798).

Exioxylon Raf. *Fl. Tellur.* 4: 85 (1838). — Apparently based upon *Echiochilon* Desf. (1798).

Leurocline Moore, *Jour. Bot.* 39: 257, *t. 424* (1901). — Type species: *L. lithospermoides* Moore.

Echiochilopsis Caballero, *Trab. Mus. Nac. Cien. Nat. Madrid, Bot.* 30: 10, *t. 2* (1935). — Type species: *E. coerulea* Cab. (= *Echiochilon chazaliei* (Boiss.) Johnston).

Tetraedrocarpus O. Schwartz, *Mitt. Inst. allgem. Bot. Hamburg* 10: 212 (1939). — Type species: *T. arabicus* O. Schwartz.

Plant usually perennial, with widely spreading erectly or ascendingly branched frutescent old stems, herbaceous and annual in one species only, bearing sparse to abundant strongly to loosely appressed hairs on stems and leaves and usually a few spreading hairs on the leaf margins, the hairs on the leaves frequently arising from well developed mineralized discoid bases, surface of the herbage glaucescent in a few species and bearing abundant minute stiped glands in two others; leaves all cauline and prevailingly alternate, the lowest on the shoot smaller than those directly above and always opposite, leaves all opposite only in one species; leaves thickish, firm or somewhat succulent, narrow and elongate and usually without visible veins or midrib, tending to be loosely conduplicate or have the margins somewhat involute, inflorescence few- to many-flowered, bracteate throughout, consisting of flowers interspersed among the leaves along the outer half of the leafy shoot or of flowers aggregated into an erect, elongating, racemose cluster terminating the leafy stems and branches, never developing a distinctly scorpioid apex; calyx 5-fid, subsessile or with a short stout strict pedicel; lobes erect, usually elongate, oblong to lanceolate or oblanceolate, all similar or nearly so or in a few species very unequal, distinct or rarely united at the very base to form a very short tube, when unequal the smallest lobe always adaxial and the largest lobe always one of the abaxial pair; corolla white, lilac, blue or reddish purple, in some species light colored at anthesis and then changing to blue or purple in age, short to elongate, hypocrateriform, funnelform or funnelform-tubular, small to moderately large, radially symmetric to very strongly zygomorphic, outside commonly strigulose or villulose but sometimes glabrous or bearing only minute stipitate glands; corolla-limb horizontal (i.e., on all sides diverging at 90° from the long axis of the corolla) or weakly to extremely oblique (i.e., highest on the adaxial side and sloping downward, gently to very steeply, towards the low abaxial side), in zygomorphic corollas the 2-lobed adaxial

side always best developed and its lobes always erect, the forward lip in zygomorphic corollas usually spreading or loosely decurved and evidently 3-lobed but in one species reduced to a very narrow recurved unlobed rim; corolla lobes rounded, obovate to ovate or semicircular, all similar or differing more or less in size and shape, sometimes with conspicuous dichotomous veining or with crisped margins, in radially symmetric corollas the lobes all similar and equally spreading or sometimes the 2 adaxial lobes less widely spreading than the other three, in distinctly zygomorphic corollas the 2 erect adaxial lobes the largest, the medial abaxial lobe the smallest, and the 2 anterior laterals intermediate in size; corolla-throat densely villose inside with white or yellow hairs, bearing neither appendages nor glands, gradually expanding or campanulate, usually about as long as the tube, in zygomorphic corollas most prolonged on the adaxial side, most swollen on the abaxial side, and the upper margin evidently oblique; corolla tube without a well developed annulus, the latter absent or represented by an indistinct broad, very low-convex annular ridge which is either glabrous or inconspicuously villulose; stamens 5, arising from among the abundant hairs deep in the throat, all borne at the same distance above the corolla-base or with the adaxial stamen highest, the forward abaxial pair lowest, and the abaxial lateral pair at an intermediate level; filaments equal or unequal, from very short (merely unguiculate) to almost as long as the anther; anthers affixed above the middle, included or short-exserted, elongate, narrowly oblong with rounded summit, base rounded with short sinus, connective very narrow and inconspicuous; thecae becoming explanate and reflexed after dehiscence, the backs of the open thecae juxtaposed and the flattened pallid inner surfaces of the thecae parallel and facing in diametrically opposite directions, the empty anthers accordingly very pale, very strongly compressed laterally and bearing the filament-attachment in a deep cleft on the narrow dorsal side; pollen usually 2-colpate, and commonly more or less bilateral, 13–21 μ high and 15–24 μ broad, subcylindric and commonly broader than long, polar profile circular to elliptic or rhombic, lateral profile quadrate to transversely oblong; pollen rarely 3-colpate, 13–16 μ high, 15–23 μ broad, polar profile circular or 3-sided, lateral profile transversely ovate or elliptic; gynobase from a broad base medially and abruptly narrowed into a usually 4-sided slender attenuate upward prolongation (usually equalling the nutlet in height), the central upward prolongation commonly buttressed below the middle by 4 triangular wings, the nutlets usually attached in the (frequently excavated) angle between the wings of the gynobase and higher up along the usually sulcate side of the upward prolongation of the gynobase, in one species the nutlet not attached between the buttresses of the gynobase but only along the crest of the buttresses and, higher up, along the sides of the central upward prolongation; style short to moderately elongate, usually extending up only to the base of the corolla-throat, never exserted, terminating the central upward prolongation of the gynobase, slender, entire or, in one species, very shortly bilobed at the apex,

and when you go with out of a way I will be
home before you come back to town. I will be
out all day and will be home in time to have

you come to my room to have dinner & go with

me & we will go to the park & we will go into the

associated. *Echiochilon* as redefined is distinguished from the monotypic *Sericostoma* by the form and position of the stigmas, the form of nutlet-attachment, form of gynobase, valvate rather than imbricate sepals, position of stamen-attachment, etc., characters certainly much more significant than those involving the relative size of corolla and the degree of zygomorphy which alone distinguished the two genera before redefinition.

The corollas of *Echiochilon* may have a pronounced bilateral symmetry or may show little or no departure from the radial symmetry that prevails in the flowers of most Boraginaceae. In four species of the genus, *E. longiflorum*, *E. lithospermoides*, *E. chazaliei*, and *E. fruticosum*, the corollas are very strongly zygomorphic, being conspicuously prolonged dorsally and having an excessively oblique limb. In all these species the stamens are affixed in three superposed levels within the irregular corolla. The most extreme zygomorphy is that of *E. longiflorum*. Whereas the other species have the forward (abaxial) lip of the corolla more or less evidently 3-lobed, *E. longiflorum* has only the two rear corolla lobes well developed, the forward lip of the corolla being represented only by an inconspicuous, narrow, recurving, unlobed margin.

In contrast to the four just discussed, such species as *E. collenettei*, *E. arenarium*, *E. jugatum*, *E. vatkei*, *E. albidum*, *E. nubicum*, *E. verrucosum*, and *E. thesingeri* have corollas that are actinomorphic or practically so. Among this group of species only *E. verrucosum* has stamens that arise at different levels within the corolla. All the others have stamens arising from the wall of the throat all at the same level above the corolla-base. Their flowers have radial symmetry, not only in form of corolla but also as to size and attachment of the members of the androecium.

The remaining species of *Echiochilon* have corollas transitional in various degrees between the strongly bilateral and the radially symmetric corollas just mentioned. The corollas of *E. kotschyi*, *E. strigosum*, *E. persicum*, and *E. arabicum* have only inconspicuously zygomorphic corollas. These deviate from radial symmetry only in having the two adaxial lobes somewhat larger and less spreading than the other three lobes. The stamens are borne on the corolla in three superposed levels in all four species. More pronounced zygomorphy is present in the corollas of *E. adenophorum*. In that species the corolla-limb is distinctly oblique, but not so extremely so as in *E. longiflorum* and its relatives. The two lobes of the adaxial lip are large and erect and evidently larger than the three spreading, evidently smaller lobes of the anterior lip. The stamens are affixed at unequal heights within the corolla-throat.

Past authors have repeatedly compared the irregular corollas of *Echiochilon* with those of *Echium* and, indeed, have frequently classified the two genera together because of their zygomorphy. Though the corollas in these genera are both irregular, they are organized with fundamentally different planes of symmetry, cf. *Jour. Arn. Arb.* 35: 165 (1954).

The orientation of the strongly zygomorphic corollas of *Echiochilon longiflorum*, *E. lithospermoides*, *E. chazaliei*, and *E. fruticosum* can be es-

tablished readily and with accuracy by reference to identifiable lobes of the calyx. In the species mentioned the calyx-lobes are extremely unequal with the shortest lobes always having the adaxial position and the largest lobe always being one of the two abaxial lobes. Following the system of numbering adopted by Eichler, the largest lobe is No. 1, the smallest lobe is No. 2 and lobe No. 3 is the companion of No. 1 on the abaxial side of the calyx. A close examination of the flower shows very clearly that the medial plane of symmetry in the flower passes through calyx-lobe No. 2 and between calyx-lobes Nos. 1 and 3, and also between the two rear (adaxial) corolla-lobes and through the middle lobe of the three-lobed forward lip of the corolla. The corolla of *Echiochilon* is not resupinate as in *Echium* cf. Jour. Arnold Arb. 34: 287 (1953), and its rear (adaxial) lip is bilobed rather than trilobed. The stamens, when borne at differing altitudes within the corolla, always have the odd, unpaired member borne on the adaxial side and always affixed higher above the corolla-base than the other four stamens. In *Echium*, although the stamens are also borne at unequal heights in the corolla-throat, the odd, unpaired stamen is borne not on the adaxial but on the abaxial side of the corolla and is the lowest rather than the highest of the five stamens. The differences between the corollas of *Echiochilon* and *Echium* are more significant than are the similarities. This is perhaps not surprising, for if one considers all characters in corolla, stamens, pollen, stigmas and nutlets, it seems impossible that the two genera could be immediately or even closely related.

Characteristic of the genus is 2-colpate, bilaterally symmetric pollen. This anomalous form of pollen has been observed in every species of the genus. Usually it is the only type of pollen produced, but in a few species it may be observed mixed in various proportions with 3-colpate pollen and even in mixtures in which the 3-colpate type may overwhelmingly predominate. Among the sixty-two samples of pollen studied, the largest quantity of 3-colpate grains has been observed in the samples representing *E. jugatum*, *E. persicum*, and *E. thesigeri*. Occasional 3-colpate grains were found intermixed with the almost exclusively 2-colpate pollen of *E. kotschyi* and *E. vatkei*. Only 2-colpate pollen was noted in the other species of the genus. Similar 2-colpate pollen occurs in *Sericostoma*, but is known from no other genus of the Boraginaceae.

The bicolpate bilaterally symmetric pollen of the genus is elliptic, rhombic-elliptic or nearly circular in polar profile. A slight prominence or roughening in the periphery usually marks clearly the location of the two colpi. The colpi are diametrically opposite when the silhouette is circular and usually located at the far ends when elliptic or rhombic. Only in the elongate grains of *E. lithospermoides*, *E. longiflorum*, and *E. fruticosum* are the colpi borne at the middle of the broad side and not at the far ends of the grains.

In lateral profile the grains are quadrate or rectangular and tend to be broader than high. The upper and lower edges in lateral profile are usually straight and parallel, which indicates that the grains are truncate and plane on top and bottom. The vertical edges of the quadrate or rectangular lat-

eral silhouette differ from the top and bottom edges in being very moderately but still distinctly convex. The two colpi are short, vertical and equatorial and are borne on opposite sides of the usually bilaterally symmetric grain.

The grain as a three-dimensional object can be described as subcylindrical, flattened on the upper and lower ends and as broad as long or slightly broader than long. The grains are usually swollen laterally in the vicinity of the two colpi and, accordingly, are usually broader along the diameter connecting the two colpiferous faces than along the diameter between the non-colpiferous faces. Because of this, the polar profile of the grain may vary from nearly circular to elliptic or somewhat rhombic in outline. Furthermore, as a result of the described modifications the grains may lose their basic radial organization and assume a moderate but very definite bilateral symmetry.

The bilaterally symmetric bicolpate grains appear to be a modification of the tri-colpate. In polar profile the 3-colpate grains of *Echiochilon* may appear circular with the location of the colpi weakly marked on the periphery or it can be distinctly three-sided with the colpi evident on each of the three angles. In lateral outline the 3-colpate grains are transversely ovate or elliptic and are accordingly broader than high. The grain, as a three-dimensional figure, accordingly, is broader than high and is more or less convex on the upper and lower surfaces. The three colpi are vertical and equatorial. The pollen consists of three equivalent radial sectors. By the suppression of one of these sectors the bicolpate pollen of *Echiochilon* and *Sericostoma* has been formed.

The bicolpate grains in *Echiochilon* when expanded in lactic acid have quadrate or rectangular colpiferous faces, in most species, measuring 16–19 μ in width and 13–16 μ in height. The maximum size occurs in the grains of *E. chazaliei* in which the colpiferous face measures 22–24 μ wide and 18–21 μ high. In the small grains of *E. strigosum* the face is 15–16 μ wide and 13–15 μ high.

In polar profile the grains may be circular or nearly so and 14–16 μ in diameter or be elliptic or rhombic and measure 16–21 μ long and 14–16 μ wide. The grains of *E. chazaliei*, the largest in the genus, have a polar profile 24–28 μ long and 21–24 μ wide.

Tricolpate grains have the lateral silhouette transversely ovate or elliptic and measuring 16–19 μ wide and 13–16 μ high. The polar profile, three-sided or nearly circular, is 15–23 μ broad.

The stigmas of *Echiochilon* are unusual among the Boraginoideae, being transversely prolonged and usually forming a band about the style just below its apex. In *Sericostoma* the two stigmas are subglobose or short-oblong and as long as broad or longer than broad. They always project upward well above the sterile tip of the style. In *Echiochilon* the two stigmas are transversely elongate, being 3–6 times broader than long. The two stigmas usually have their ends touching and sometimes partially confluent. Together they form a narrow, usually slightly sinuous, pallid swollen vesicular band around the style just below its apex. These stigmas un-

questionably have a lateral and subapical position on the stylar column. The sterile apex of the style, in a variety of forms, is evidently prolonged above the stigmatic band. In one species the style is bilobed at the apex and a stigma partially encircles each of the short lobes just below the short, convex, sterile apex. The stigmas remain distinct.

In most of the small-flowered species (Nos. 8-17), the tip of the style is broad and low-convex and usually projects above the stigmas for a height equal to about half the width of the stigmatic band. This sterile summit may be simply convex or may be obscurely bilobed. In *E. collenettei*, the apex is most prolonged, being short-cylindric and entire, or sometimes bilobed. In *E. chazaliei* the apex is high convex, being at least hemispheric, and usually bears a small terminal depression at the very summit. In *E. arenarium* the stylar apex is divided into a pair of erect, usually very slightly unequal, attenuate lobes having a length equalling several times the width of the stigmatic ring. The elongate sterile tips of the style, prolonged well beyond the annular stigmas, combine in *E. arenarium* and *E. collenettei* to produce a structure very suggestive of the stigmatic head developed in *Heliotropium*. The condition has its closest parallel among the Boraginoideae in *Buglossoides*, cf. *Jour. Arnold Arb.* 35: 40 (1954) and 35: 161 (1954).

The style and stigmas of *E. longiflorum*, *E. lithospermoides* and *E. adenophorum* are the most specialized in the genus. The summit of the style, encircled by the stigmas, is enlarged, very oblique and bilaterally symmetric. The style just below its summit abruptly increases in diameter two- or rarely three-fold and is there encircled by the stigmas. The style with its abruptly thickened summit is somewhat suggestive of a nail with a broad head. The "head" of the style, however, differs from that of a nail in being oblique rather than horizontal. From the low rear (adaxial) margin its slope upward at an angle of 30°-60° towards the high forward (abaxial) margin. The band of stigmatic tissue on the margin of the "head" is also oblique. On the broad, decidedly sloping summit of the stylar head are borne a pair of sterile stylar apices of unusual form. Viewed from above the two apices are separate and parallel and lanceolate or ovate in outline. Together they are frequently very suggestive of the hoof of a goat. Viewed from the side they increase in height as they extend across the stylar head from the rear towards the forward margin. They are most conspicuous on the high forward side of the stylar head and broadest and tallest there. They are moderately developed in *E. adenophorum* and best developed in *E. longiflorum* and *E. lithospermoides*. These three species all have very strongly zygomorphic corollas. The asymmetric and oblique heads of the style, however, are not an invariable accompaniment of strong zygomorphy. Although the corolla of *E. chazaliei* is very oblique and zygomorphic, its style is not enlarged at the apex, its stigmas form a horizontal band, and the style has a simple, high-domed apex.

The style and stigmas of *E. fruticosum* have unique features. Differing from other species in the genus, *E. fruticosum* has a style which is distinctly bilobed. Each of the very short stout lobes is partially embraced

by a transversely elongate stigma borne laterally just beneath the rounded apex of the lobe. Separated on lobes of the style that tend to diverge in age, the stigmas of *E. fruticosum* remain evidently distinct and give no appearance of being joined to form a continuous stigmatic band entirely surrounding the style as do the stigmas in other species of the genus. They are somewhat suggestive of the stigmas in the genus *Sericostoma* but are borne lateral and subapical and not terminal on the style as in that genus.

The nutlets of most of the species of *Echiochilon* are broadly lanceolate to ovate in dorsal outline and most of them are rather plump. In many of the species they are paired, being bent either left or right, so that, of adjacent nutlets, one is the mirror image of the other.

The attachment of the nutlets is essentially lateral. The gynobase is usually about as long as the nutlet. The nutlet has its principal area of attachment in a broad, usually more or less triangular areola which is borne on the ventral side of the nutlet-base at the lower end of the vertical ventral keel, sometimes below and oblique to the keel but usually in the same plane as the keel. Only in *E. chazaliei* and *E. adenophorum* is the attachment-areola so excessively oblique as to become almost basal on the nutlet and even nearly horizontal. From the attachment-areola a linear or attenuate sulcus is usually prolonged up the center of the nutlet along the crest of the ventral angle of the nutlet. This sulcus is the open ventral suture of the nutlet. The margins of the suture are concrescent only near the nutlet apex. In most species the suture is open to well above the middle of the nutlet body and frequently open almost all the way to the nutlet apex. In a few species such as *E. chazaliei*, *E. adenophorum* and *E. arenarium*, however, it may be closed for much of its length, but closed only by having the margins of the suture merely touching or shortly overlapped, and very definitely not by the fusion of the margins.

The pit which represents the end of the broken funicular canal is located in the attachment areola, usually in or near the upper corner of the areola and consequently beneath the lower end of the ventral keel. The course of the canal as it leaves the nutlet is vertical and usually more or less in line with the crest of the ventral keel above it.

Only two species develop nutlets especially noteworthy as to form. The eastern variety of *E. fruticosum* has plump, lanceolate nutlets. In the typical phase of the species from North Africa, however, the nutlets are not straight, erect and lanceolate. They are bent and have their broad lower half diverging from the vertical ventral sulcus and the gynobase at an angle of almost 90°. The back of the nutlet is incurved and saddle-like in lateral outline. I know of no other borage having nutlets which are bent 90° at the middle and which have the upper half vertical and affixed to the slender gynobase while the lower half is spreading and divergent from the floral axis. Bent nutlets occur in the Lithospermeae, cf. Jour. Arnold Arb. 35: 161 (1954), but among these plants it is the lower half of the nutlet which is vertical. Furthermore, the bending of the nutlet in the Lithospermeae is inward over the floral axis and not outward and away from it as in *E. fruticosum*.

The nutlet of *E. longiflorum* has a number of unusual features. The broad base of the nutlet is shortly bilobed, has a deep medial sinus and is definitely cordate in outline. The nutlets viewed dorsally are decidedly heart-shaped. So deep is the basal sinus that the seed inside the nutlet has bilobed cotyledons. The broad nutlet has no large attachment-areola. It is attached to the slender erect gynobase only along a lineate sulcus. This groove, an open suture, extends down the vertical ventral keel to above the sinus on the nutlet-base where it abruptly and widely forks. The branches of the sulcus are at first divaricate but promptly decurve on the oblique lower surfaces of the nutlet venter and finally end low down on the oblique side of the two basal lobes of the nutlet. In most species of the genus the nutlet-areole is attached in the angle at the base of the gynobase between the wings buttressing the base. In *E. longiflorum*, however, the attachment sulcus is affixed to the sides of the subulate gynobase and, below the fork, along the crests of the buttressing wings and not at all in the angle between them.

KEY TO THE SPECIES OF ECHIOCHILON

Corolla glabrous on outer surface; foliage tending to be succulent and glaucous.

Plant annual; nutlets cordate, having a pronounced basal sinus. 1. *E. longiflorum*.

Plants perennial, frutescent; nutlets ovoid, not cordate.

Leaves, bracts and calyx-lobes with a midrib; leaves lanceolate, apex attenuate, margin hispid-ciliate; stigmas decidedly oblique, surmounted by a bilobed tip of the style. 2. *E. lithospermoides*.

Leaves, bracts and calyx-lobes not costate; leaves thick, obovate to spatulate, apex obtuse or rounded, margins not ciliate; stigmas horizontal, surrounding the domed sterile apex of the style. 3. *E. chazaliei*.

Corolla evidently hairy outside or bearing minute stipitate glands.

Herbage bearing abundant minute stipitate glands; corolla glanduliferous outside, not hairy.

Corolla zygomorphic, limb oblique and bilabiate, filaments borne at unequal heights in the corolla-throat; stigmas very oblique, sterile tip of style inconspicuous, extremely short; nutlets with basal and horizontal attachment-scar. 4. *E. adenophorum*.

Corolla regular, limb not oblique, filaments all arising at the same distance above the corolla-base; stigmas horizontal, surmounted by the evident, somewhat cylindric sterile tip of the style; nutlets with the attachment-scar distinctly lateral and vertical. 5. *E. collenettei*.

Herbage not distinctly glanduliferous; corolla villulose or strigulose outside, not glanduliferous.

Calyx-lobes conspicuously unequal in length, commonly with blue margins; corolla 8-12 mm. long, strongly zygomorphic with a conspicuously oblique limb; style 2.5-3.5 mm. long; stigmas distinctly oblique; North Africa, Sinai and Palestine. 6. *E. fruticosum*.

Calyx-lobes equal in length or practically so, without colored margins; corolla 3–6 mm. long, radially symmetric or only very moderately zygomorphic, limb not at all oblique or only very moderately so; stigmas horizontal or somewhat oblique only in No. 7.

Style 1–3.5 mm. long, terminated in a pair of subulate sterile tips 0.2–0.5 mm. long; calyx with lobes united at the base into a short tube; coast of Italian Somaliland. 7. *E. arenarium*.

Style 0.5–1.5 mm. long, abruptly contracted into a very short broad usually merely convex sterile tip barely surpassing the stigmas; calyx-lobes not united into a short tube.

Flowers borne along the leafy stems interspersed among developed leaves, the inflorescence hence interrupted, not distinctly racemose nor unilateral.

Leaves all opposite, only the bracts alternate and these usually opposing a flower; plant silvery strigose, and indument smooth and dense; corolla 5–6 mm. long, regular; eastern and southern Arabia. 8. *E. jugatum*.

Leaves mostly alternate, only the several lowermost pairs of leaves on the shoot opposite.

Plant generously strigose, whitish or gray; corolla 5.5–6 mm. long, zygomorphic, the 2 adaxial lobes prolonged, the limb somewhat oblique and the filaments affixed at unequal heights on the corolla; style 1.5–1.7 mm. long; nutlets obscurely roughened or nearly smooth; islands of the Persian Gulf. 9. *E. kotschy*.

Plant with sparse appressed grayish hairs, greenish; corolla 3.5–4 mm. long, the limb regular and the filaments affixed at equal heights on the corolla; style 0.5–0.7 mm. long; nutlets prominently and densely verrucose; eastern British Somaliland. 10. *E. vatkei*.

Flowers borne in elongating unilateral racemose cymes; inflorescence terminating the leafy twig, bearing small bracts but not interrupted by well developed leaves.

Leaves lustrous, white, densely clad with abundant appressed snowy or silvery white hairs; northeastern Somaliland. 11. *E. albidum*.

Leaves greenish or cinereous, if distinctly pallid not clad in abundant lustrous white hairs.

Corolla distinctly prolonged on the adaxial side, the axial pair of lobes largest and the limb oblique.

Leaves small (1–6 mm. long, 0.5–1 mm. broad), becoming recurved; corolla small, 3–4 mm. long; southern Arabia. 12. *E. strigosum*.

Leaves larger (3–15 mm. long, 1–3 mm. broad), spreading or ascending.

Plant pallid, clothed with abundant appressed white or gray hairs; corolla 4.5–6 mm. long; southern Iran and Baluchistan. 13. *E. persicum*.

Plant greenish, clothed with fewer hairs and usually hispid; corolla 5–8 mm. long; southern Arabia and middle northern British Somaliland. 14. *E. arabicum*.

Corolla not prolonged on adaxial side or at most only very obscurely so; corolla limb not oblique and the lobes equal or nearly so.

Plant whitish, densely clad with pallid hairs; calyx at anthesis 2–2.5 mm. long, sessile or subsessile at maturity; style very short 0.5–0.8 mm. long; Sudan coast of Red Sea. 15. *E. nubicum*.

Plant grayish green, only moderately hairy; calyx at anthesis 2.5–3 mm. long, developing a stout strict pedicel 0.5–1.5 mm. long at maturity; style 1–1.4 mm. long.

Filaments arising from the corolla at unequal distances above the corolla-base; western Brit. Somaliland. 16. *E. verrucosum*.

Filaments within the corolla all arising at the same distance above the corolla-base; eastern and southern Arabia. 17. *E. thesigeri*.

1. *Echiochilon longiflorum* Benth. in Hook. *Icones Pl.* 13: 60, t. 1277 (1879) — near Aden, *Wykeham Perry*.

Lobostemon somalensis Franchet, *Sert. Somal.* 44 (1882) — pays des Comalis, *George Revoil* 78.

Leurocline somalensis (Franch.) S. Moore, *Jour. Bot.* 39: 258 (1901).

Echiochilon somalense (Franch.) Johnston, *Contr. Gray Herb* 73: 50 (1924).

Annual herb, erect with ascending branches, glaucous, 5–40 cm. tall; cotyledons persisting (sometimes even on the flowering plant), 6–10 mm. long, from a slender petiole 3–5 mm. long expanding into a blade 4–7 mm. wide, coarsely and conspicuously emarginate at apex, the terminal sinus 1–2 mm. deep and usually as broad, usually rounded at the base; leaves alternate or only the lowermost opposite, somewhat succulent, lanceolate, usually acute, 1–4 cm. long, 2–6 mm. broad, upper surface glabrous, lower surface bearing scattered coarse mineralized disks from which may arise short usually appressed hairs, midrib usually evident on lower surface; stems and branches terminating into elongate unilateral racemose cymes; cymes not at all scorpioid, erect, many-flowered; bracts numerous, foliaceous, gradually reduced in size upwards along the cyme; calyx with very unequal lobes, at anthesis 4–6 mm. long, borne on a pedicel 1–3 mm. long, smallest lobe adaxial, linear, 1.5–2 mm. long, 0.2–0.5 mm. wide, largest lobe abaxial 5–6 mm. long, 1–2 mm. broad; corolla lilac or pale blue, glabrous, texture not firm, 12–18 mm. long, densely white villose inside throat; limb of corolla very oblique ca. 10 mm. long, the adaxial lip prolonged, loosely recurving above the middle, its lobes 2–2.5 mm. long, the three abaxial lobes small, crowded to form the poorly developed weakly 3-lobed recurving abaxial lip of the corolla; corolla-tube 4.5–5.5 mm. long, broadest (ca. 1.3 mm. thick) 1–1.5 mm. above the base, at summit ex-

panding into an evident funnelform oblique throat which is 2–3.5 mm. thick; stamens borne at base of throat just above the narrowest part of the tube, with filaments of unequal lengths and affixed at unequal heights above the corolla-base; anthers 0.8–1 mm. long; adaxial medial filament as much as 0.8 mm. long and borne 7 mm. above corolla-base; abaxial pair of stamens with filaments 0.2 mm. long and affixed 5.5 mm. above corolla-base; lateral stamens with filaments 0.7–0.8 mm. long and affixed 6 mm. above base of corolla; gynobase with a small horizontal base (1–1.3 mm. wide) from the center of which arises a slender 4-sided vertical upward prolongation ca. 2.5 mm. long and ca. 0.25 mm. thick, terminated by a style 4–5 mm. long; stigmas strongly oblique, highest on abaxial side, surrounded by 2 prominent sterile terminal lobes (0.1–0.2 mm. long) of the style; nutlets 2.3–3 mm. long, reddish to gray-brown, usually four developing, 1.8–2 mm. broad just above the base, verrucose or irregularly tuberculate, the base broad, deeply and conspicuously cordate, the apex coarsely rostrate, venter evidently sulcate, the groove extending down from near the nutlet-tip almost to the nutlet-base, lateral and vertical, above the base very widely forked and oblique on the basal lobes of the nutlet.

ADEN: Aden, received Aug. 1900, *Dr. T. Cooke*, (K); "Aden or Perim," *J. V. Lester-Garland* (K); Aden, Feb. 19, 1900, *W. S. Birdwood* (K); Aden, 1884, *H. R. Beevor* 103 (K); Aden, only one specimen found, ca. 1 ft. tall, corolla light blue, stems and branches smooth, March 1878, *W. Wykeham Perry* 9 (Type of *E. longiflorum*, Kew).

SOMALILAND: Wardere Well, 6–10 in. tall, fl. lilac, Nov. 23, 1944, "Kabaageye," *Glover & Gilliland* 302 (K); Dubriat Mt., lat. 10°22'N., long. 45°10'E., throat and tube of corolla bright pale blue, limb pale lilac, bed of torrent, limestone, 700 ft. alt., Jan. 3, 1933, *J. B. Gillett* 4787 (K); Djibouti, 1895, *Dr. Jousseaume* (P); pays des Comalis, *Geo. Revoil* 78 (Type of *L. somalensis*, Paris).

Distinguished from all other members of the genus both by its annual habit and its cordate nutlets. The nutlets of *E. longiflorum* constitute one of the bizarre extreme variants of the boraginaceous fruit. As to their cordate body, they have a parallel only in the fruit of the unrelated *Arnebia tetragastigma* Forsk. The closest relation of our species, however, appears to be with *E. lithospermoides*. Interestingly, in that species the base of the nutlets may be obscurely depressed and hence is suggestive of an incipient state of a type of variation that could be elaborated to form a deep basal sinus such as is present on the nutlets of *E. longiflorum*. I have seen both the type of *E. longiflorum* and of *Lobostemon somalensis*. They are representative of the same species without doubt. The plant is a desert annual which is not only rare but also one that has been encountered only in very limited quantity.

2. *Echiochilon lithospermoides* (S. Moore) Johnston, Contr. Gray Herb. 73: 50 (1924).

Leurocline lithospermoides S. Moore, Jour. Bot. 39: 257, t. 424, f. 1 (1901) —
Brit. East Africa: Leikipia, June 1893, J. W. Gregory; Gof at 3800 ft. and
between Lé and Tocha, 1898, Lord Delamere.
Lobostemon lithospermoides (S. Moore) Baker, Fl. Trop. Africa 4²: 60
(1905).

Plant suffrutescent, perennial, 1–4 dm. tall, freely and ascendingly branched; stems 1–10 dm. long, becoming shrubby and decumbent in age; herbage glaucous; leaves lanceolate, 1–3 cm. long, 2–5 mm. wide, broadest above the sessile base and gradually narrowed to the sharply acute or acuminate apex, upper surface usually glabrous, lower surface with mineralized pustules or short stout spreading hairs arising from bulbous bases, usually more or less evidently costate, margin usually coarsely hispid-ciliate; inflorescence an erect unilateral racemose cyme, elongating in age, 1–3 dm. long, 10–50-flowered, terminating the stem and branches, bracts numerous, evident, foliose, lowermost similar to the uppermost leaves, very gradually reduced upward along the cyme; calyx subsessile or in age with strict pedicel 1–2 mm. long, with very unequal lobes; lobes distinct, hispid-ciliate, largest lobe abaxial, lanceolate, attenuate, ca. 8 mm. long and ca. 1.3 mm. broad above the base, becoming twice as large and costate at maturity; smallest lobe adaxial, ca. 4 mm. long and 0.4–0.5 mm. broad, twice as large at maturity; inner surface of calyx lobes glabrous, outer surface pustulate or bearing some stout hairs arising from bulbous bases; corolla reddish purple, 12–15 mm. long, strongly zygomorphic, glabrous outside, below the middle tubular and above the middle expanding into an extremely oblique funnelform throat and limb; corolla-tube usually ca. 2 mm. in diameter at the very base, constricted (to 1.3–1.5 mm. thick) 4.5–6 mm. above the base and then expanding into the throat; limb 7–9 mm. in diameter; corolla-lobes rounded, the two adaxial lobes vertical, erect, 2.5 mm. broad, the three other lobes less well developed, the single anterior lobe horizontal; inside of corolla densely villulose in a zone usually extending from 4 to 6.5 mm. above the corolla base, hairs 0.2–0.3 mm. long, white or slightly yellowish; inside of corolla-throat bearing only scattered hairs which may be 0.3–0.4 mm. long, base of tube without annulus and glabrous; anthers 1–1.3 mm. long, elongate, slightly arcuate, emarginate at base, borne at unequal heights just above the narrowest part of the corolla at the base of the throat; adaxial anther borne on a filament 0.6–0.7 mm. long arising ca. 6.5 mm. above the corolla-base; adaxial lateral pair of anthers borne on filaments 0.3–0.4 mm. long arising ca. 5.5 mm. above corolla-base; abaxial pairs of anthers borne on filaments 0.2–0.3 mm. long arising only 5 mm. above corolla-base; gynobase at maturity 1.5–2 mm. tall, pyramidal, 1–1.3 mm. broad at base, sides usually excavated; style 3–4 mm. long at anthesis, stigmas oblique, surmounted by 2 laterally compressed sterile tips of the style which are usually most prominent on the high abaxial side of the stigma; nutlets 1–4 developing, 2–2.4 mm. long and nearly as broad, plump, reddish, back usually tuberculate and more or less tumulose, venter angulate, bearing a triangular areole (ca. 1 mm.

wide) which contracts into a linear or (more commonly) attenuate sulcus that extends upward almost to the nutlet-apex; areola ventral, usually with prominent scar-tissue, more or less oblique.

KENYA: Banaisa, North Frontier dist., fl. red, June 27, 1951, *Kirrika* 92 (G, K); Rumuruti, K. 3, *Coryndon* 6865 (K); Rumuruti, northeast slope of Aberdares, 7000 ft. alt., fl. pink or red, *W. J. Dowson* 551, 554 (K); Rumuruti, common locally, grassland with scattered trees, Aug. 12, 1952, *Bogdan* 3519 (K); 50 miles southeast of Nairobi, dry soil in shade, fl. "aster purple," leaves "bice green," 5000-7000 ft. alt., July 13, 1923, *A. G. Curtis* 757 (G); Mile 20, between Laitokitak and Kijiado, N. Kilimanjaro, tufted grassland, shallow red soil above limestone, plant tufted, about 2 ft. tall and 2 ft. in diameter, Sept. 1952, *P. R. O. Bally* 8323 (K, Fl).

ETHIOPIA (Boran): Road between Moyale and Mega, $30^{\circ}44'N$, $38^{\circ}50'E$, open scrub in red sandy loam, spreading shrublet 40 cm. tall, corolla reddish purple fading to blue-purple, 4200 ft. alt., Nov. 10, 1952, *J. B. Gillett* 14191 (G, K); in deserto Banas, July 14, 1893, *Ruspoli & Riva* 1634 (882) (Fl); between Mega and Malca Guba, April 26, 1939, *R. Corradi* 6206 (Fl); Mega, April and Sept. 1939, *R. Corradi* 6389, 6399, 6401 (Fl); Javello diciivi de Quota Littorio, fl. atropurpurei, April 18, 1937, *G. Cufodontis* 479 (Fl); Foresta de Neghelli, Aug. 23, 1937, *A. Vatova* 231 (Fl); Foresta di Neghelli, Sept. 27, 1939, *R. Corradi* 8237 (Fl); Neghelli, Sept. 10-29, 1939, *R. Corradi* 6230, 6284 (Fl).

A plant of desert grasslands which ranges from southern Ethiopia south through northern and eastern Kenya. It is known from a few stations south of the equator and accordingly is the most southerly ranging member of its genus. The species is readily recognizable and very distinct. It appears to have close relations only with *E. chazaliei* and *E. longiflorum*. In having relatively large, plump, dark reddish nutlets and sharply acute or acuminate, usually costate, leaves, bracts, and calyx-lobes, it is distinguishable from all other members of the genus.

3. *Echiochilon chazaliei* (Boiss.) Johnston, Contr. Gray Herb. 73: 50 (1924).

Lithospermum chazaliei Boiss. Jour. de Bot. 10: 220 (1896) — Cape Blanc, May 1895, *M. de Dalmas*.

Leurocline chazaliei (Boiss.) Bonnet, Bull. Soc. Bot. France 58: 38 (1911).

Leurocline mauritanica Bonnet, Bull. Mus. Hist. Nat. Paris 14: 403 (1908) — near Port Etienne, 1908, *R. Chudeau*.

Echiochilopsis coerulea A. Caballero, Trab. Mus. Nac. Cien. Nat. Madrid, Bot. 30: 10, t. 2 (1935) — inter ora fl. *Tazarut* et promontorio *Non* dictis, July 11, 1934, et ad oram fl. *Assaka* dicto, July 13, 1934, *Caballero*.

Plant fruticose, perennial; stems 5-35 cm. long, erect or ascending or decumbent, loosely and dichotomously branched, 1-5 mm. thick, sparsely strigose or nearly glabrous, in age albescens and eventually decorticating; leaves mostly alternate, only the lowest ones on the shoot opposite, oblanceolate or oblance-obovate, fleshy, glaucous, bearing scattered coarse short appressed hairs arising from discoid bases, 4-18 mm. long, 2-5 mm. broad,

apex rounded, base cuneate, without evident midrib or nerves; cymes 3-8-flowered, leafy bracted, erect, terminating the leafy branches; calyx 5-parted, 6-8 mm. long at anthesis, becoming 8-15 mm. long at maturity; calyx-lobes extremely unequal, oblong or oblanceolate, not costate, bearing scattered appressed hairs with discoid bases, tip rounded; smallest calyx lobe adaxial, 2-4 mm. long, ca. 0.5 mm. broad, largest lobes abaxial 7-13 mm. long, 1-2.5 mm. broad; pedicel stout, 1-4 mm. long; corolla violaceous or mauve, outside glabrous, 11-21 mm. long, limb very strongly oblique, 10-20 mm. long, margin frequently crisped, two rear corolla-lobes erect 3-5 mm. long and 2.5-5.5 mm. broad, forward middle lobe 2.5-5.5 mm. long and 2.5-5 mm. broad, throat oblique, narrowly funnelform, corolla-tube 6-8 mm. long 2.5-3 mm. thick, inside densely hairy above the middle, hairs in the tube and throat white; anthers 1.2-1.5 mm. long; filament of medial adaxial stamen 1.4 mm. long, affixed 6-8 mm. above corolla-base, filaments of dorsal lateral stamens 0.8-1 mm. long, affixed 5-6 mm. above corolla-base, filament of forward lateral stamens 0.8-1 mm. long affixed 4-4.5 mm. above base of corolla; gynobase very narrowly pyramidal, 3-3.5 mm. long, ca. 1 mm. thick at base; style 3-5 mm. long, sterile apex domed, high convex with a central depression, not oblique, surrounded at the base by the horizontal stigmatic band; nutlets 1-4 maturing, gray, erect, acute, 3-4 mm. long, 2-2.5 mm. broad, dorsum convex sparsely tuberculate or tumulose or somewhat lobulate-tuberculate, especially above the middle, venter obtuse, for most of its length bearing a lineate groove, attachment-areole basal, very broadly flabelliform, horizontal or oblique, its ventral angle prolonged to form a lineate sulcus which extends upward nearly to the nutlet-apex.

SPANISH SAHARA: Aguerguer, north of Cape Blanc, Jan. 22, 1937, *Murat* 1907 (G); between mouth of Rio Tazarut and Cabo Non, July 11, 1934, *Cablero* (G, Isotype of *E. coerulea*). MOROCCO: falaises du littoral de l'Ocean a l'embouchure de l'Oued Aouroura, lat. 28°50'N, March 31, 1937, *Maire* (G).

Known only from northwestern Africa where it occurs on dunes along the coast, between lat. 20° and 30°N, in Ifni, in extreme southwestern Morocco, in Spanish Sahara and in that part of Mauritania near Port Etienne. It is the most westerly ranging member of its genus. The species is a very distinct one. The closest relation is *E. lithospermooides* of east Africa. Unlike other congeners having a strongly zygomorphic corolla with an oblique limb, *E. chazaliei* has horizontal rather than oblique stigmas. The nutlets of our species are roughened principally on the back above the middle with tuberculations and papillae of unusual form. These latter are strict and have a decurrent base. A new description and illustration of the plant has been recently published by Sauvage & Vindt, Fl. du Maroc 2: 116, f. 2460 (1954). It is to be noted that the species is named not for its collector but for the yacht *Chazalie*, owned by the collector, the Count de Dalmas.

4. *Echiochilon adenophorum*, sp. nov.

Planta fruticosa 1–3 dm. alta laxe ramosa; ramis vetustioribus cortice alba decorticanti donatis; ramulis hornotinis foliosis 4–6 cm. longis 1–2 mm. crassis; internodiis 1–5 mm. longis; foliis ascendentibus alternatis (vel solum imam ad basim ramuli oppositis) glandulas minutas stipitatas abundantis proferentibus lineari-oblanceolatis laxe valdeque involutis ergo saepe plus minusve teretibus 10–25 mm. longis 1–2 mm. crassis, facie interiore glabris, facie exteriore glanduliferis sparse hispidulis (pilis rigidis 0.5–0.8 mm. longis ascendentibus vel appressis basibus discoideis praeditis); inflorescentia racemosa 5–15-flora 3–5 cm. longa; floribus congestis biseriatis bracteatis; calyce subanthesi 4 mm. longo, maturitate accrescenti 5–6 mm. longo, lobis acutis valde inaequalibus, maturitate margine incrassato et costa plus minusve incrassata donatis; pedicello 1–2 mm. longo; corolla alba elongata 10–13 mm. longa extus sparse glandulifera, tubo 5–6 mm. longo a basi imo 1–1.5 mm. crasso sursum ampliato, 1–1.5 mm. supra basim crassissime (1.7–2 mm.) deinde sursum gradatim contracto, summum ad apicem 1 mm. crasso; faucibus infundibuliformibus 4–5 mm. longis margine superiore satis obliquis 3.5–4 mm. diametro, intus pilis albis vestitis; lobis inaequalibus integris rotundis, duobus adaxialibus erectis 1.8 mm. longis late ovatis, tribus anterioribus patentibus 1 mm. longis 1.5–1.8 mm. latis; antheris ca. 1.8 mm. longis inclusis; filamentis 0.1–0.2 mm. longis aequilongis; filamento postico ca. 6.5 mm. supra basim corollae affixo; filamento duobus anticis ca. 5.5 mm. supra basim corollae affixis; filamentis duobus lateralibus intermediis 6 mm. supra basim affixis; gynobasi 1.5–1.7 mm. alto a basi 1 mm. lato sursum abrupte attenuato; stylo 4–5 mm. longo supra stigmata valde obliqua apicibus sterilibus inconspicuis latis sed perbrevibus donato; nuculis saepe solum 1–2 maturantibus erectis vel parce incurvatis ca. 2 mm. longis et 1.4 mm. latis pallide rubescensibus vetustioribus plus minusve cinereis, supra medium crasse rostratis, infra medium satis compressis, dorse supra medium evidenter tuberculatis et tumulosis, infra medium conspicue laevioribus inconspicue tuberculatis et tumulosis subplanis; ventre nuculae late obtuso sulcum lineatum angustum medio-longitudinalem haud crassi-marginatum proferenti; cicatrice nuculae basali ferè horizontali 1 mm. lata.

BRITISH SOMALILAND: rocky slopes of Goldither at 400 ft., behind Karin near Beibera, Berbera District, limestone, woody herb up to 1 ft., "sintar," April 24, 1945, *P. E. Glover & H. B. Gilliland* 1181 (Type, Brit. Mus.; Isotype, Kew).

A very distinct species which is notable for its elongate, very strongly involute leaves, its glanduliferous herbage and its elongate, moderately but distinctly zygomorphic corollas. Along with *E. collenettei*, the species seems transitional between the group of species with very strongly zygomorphic, extremely oblique, usually elongate corollas and that with short, inconspicuously oblique, or more or less perfectly symmetric, relatively short corollas. In *E. adenophorum* the summit of the throat is less than 1 mm. longer on the adaxial side than on its forward side. The throat, ac-

cordingly, is very much less oblique than in the corollas of such species as *E. longiflorum*, *E. lithospermoides*, *E. chazaliei* and *E. fruticosum*. Externally the zygomorphy in our plant is manifest most by the dorsal swelling of the throat and in the enlargement of the two adaxial lobes.

Though certainly very distinct, *E. adenophorum* appears to be most closely related to *E. collenettei*. It differs from the latter species in having strongly involute leaves which are usually terete and have the upper leaf-surface completely hidden by the inrolled margins of the leaves. The corolla of *E. adenophorum* also differs in being glanduliferous but not hairy outside and in being distinctly zygomorphic with the limb oblique, the corolla lobes unequal and the stamens affixed at unequal heights in the throat. The style also differs in having very poorly developed sterile tips surmounting the very strongly oblique stigmas. The nutlets differ also in being basifixated.

According to the label, the plant is said to come from "Karin near Berbera." Perhaps Karin or Karrin on the coast 100 km. east of Berbera is intended, being designated as "near Berbera" to distinguish it from Karin or Carin, a well-known locality just east of the eastern boundary of British Somaliland, which is located nearly 500 km. east of Berbera.

5. *Echiochilon collenettei*, sp. nov.

Planta frutescens ascendenter ramosa 25 cm. alta; ramis annotinis albis vetustioribus decorticatis; ramulis hornotinis 0.5–1.5 mm. crassis foliis congestis ascendentibus vestitis; foliis alternis crassiusculis 5–10 mm. longis 0.8–1.2 mm. latis oblanceolatis haud costatis subplanis vel satis conduplicatis utrinque glandulas stipitatas abundantis gerentibus, subtus basim versus cuticula calcarea alba donatis alibi pilos rigidos e basi discoideo erumpentis 0.5–0.9 mm. longos haud abundantis ascendentis vel appressos gerentibus; inflorescentia pauciflora, floribus 1–5 apicem versus ramulorum inter folia gestis; calyce sub anthesi 4.5 mm. longo mox 6 mm. longo, lobis subaequalibus 1–1.5 mm. latis glanduliferis pilos paucos e basi discoideo erumpentis proferentibus vetuste costatis; corolla alba elongata sub hypocrateriformi 13–15 mm. longa radialiter symmetrica, tubo 5–6 mm. longo extus glandulifero intus fere ad basim minutissime villuloso, faucibus infundibuliformibus 5–6 mm. longis ca. 3 mm. crassis intus flavovillosis, limbo horizontaliter patenti haud obliquo, lobis subhomomorphis triangulare-ovatis 2–3 mm. longis utrinque albo-villulosis margine crispatis; antheris 1.2–1.4 mm. longis; filamentis aequalibus 0.1–0.2 mm. longis 7.5–8 mm. supra basim corollae affixis; gynobasi pyramidali 1.1–1.5 mm. alta basi 1.1–1.3 mm. lato; stylo 3.5–4.5 mm. longo supra stigmata horizontalia apicem sterilem breviter cylindraceum truncatum vel plus minusve bilobatum 0.1–0.2 mm. longum 0.1–0.15 mm. crassum gerente, nuculis verrucosis 2 mm. longis 1.5 mm. latis dorso convexis ventre obtusis carinatis, cicatrice laterali verticali triangulari ca. 0.6 mm. lata prominenti sursum in sulcum crasse marginatum attenuatum abrupte producta.

ITALIAN SOMALILAND: Karin, lat. $10^{\circ}57'N.$, long. $49^{\circ}24'E.$, stony ground in dry stream bed, 900 ft. alt., plant 9 in. tall, fl. white, scarce, Oct. 29, 1929, C. N. Collenette 196 (Type, Kew).

This very well-marked species is known only from a single collection originating in northernmost Italian Somaliland just east of the British Somaliland boundary, cf. Collenette, Kew Bull. 1931: 403, 410 (1931). Unhappily, only a single corolla has been available for dissection. The stamens are borne on filaments of equal length which are all affixed at the same distance above the corolla-base. The corolla is regular or practically so, at most having the lobes differing very slightly in size. The relationships of the plant are probably closest with the very distinct *E. adenophorum* of northern middle British Somaliland. Both species have glandulariferous herbage and an elongate, somewhat trumpet-shaped corolla. Our plant differs, however, in having regular, non-zygomorphic corollas, as well as stouter, more plump nutlets, a lateral rather than basal nutlet-attachment, nearly equal calyx-lobes, smaller, nearly flat leaves, etc. The nutlets are very similar to those of *E. verrucosum*.

6. *Echiochilon fruticosum* Desf. Fl. Atlant. 1: 167, t. 47 (1798) — habitat prope Kerwan in regno Tunetano.

Echiochilon fruticosum var. *marginatum* F. Buxb. Verhandl. Zoo.-Bot. Ges. Wien 76: 61 (1927) — Aïn Ghrasesia, Tunisia, 1913, Janchen & Vierhapper.

Plant fruticose, pale; stems slender, decumbent, loosely branched, leafy branchlets 1–2 mm. thick, bearing appressed hairs ca. 0.5 mm. long; leaves all caudate, numerous, lanceolate, small, 2–10 mm. long and 0.5–2 mm. broad, acute, lacking evident midrib or veins, bearing appressed hairs on both surfaces; lowermost leaves opposite; cymes racemose, slender, erect, not at all scorpioid, 5–15 cm. long; bracts numerous, foliaceous, frequently with blue margins; calyx 4.5–5 mm. long, subsessile; calyx-lobes very unequal, lanceolate, frequently with blue margins, shortest lobe adaxial, 2–3.5 mm. long and 0.5 mm. wide, largest lobe 3.5–4.5 mm. long and 1 mm. wide; corolla blue, strongly zygomorphic, 8–12 mm. long, conspicuously hairy outside; limb very oblique, 8–10 mm. long and 4–6 mm. broad, with a spreading crisped margin 1–2 mm. wide, upper adaxial end of limb evidently 2-lobed (lobes erect 1.5–2.5 mm. long and broad) but less evidently lobed on the lower abaxial lip; tube and throat together 4.5–6 mm. long, 0.8–1 mm. thick at base, ampliate upwards and becoming 1.5–1.8 mm. thick (1–1.5 mm. above base of tube) and then constricted to 0.9–1.3 mm. thick (at 2.5–3 mm. above base) and finally swelling to 2.3 mm. (at 4–4.5 mm. above the base) at the level of the base of the forward corolla-lip; inside of corolla with an abundance of white or gray hairs just above the constriction of the corolla-tube, sparingly hairy in the throat and on the limb; anthers 1–1.2 mm. long; adaxial filament longest and borne highest in the throat, 0.4–0.6 mm. long, affixed 4.5 mm. above corolla-base; adaxial lateral pair of filaments borne 0.3–0.5 mm. below upper filament, 0.1–0.3

mm. long; forward pair of filaments borne 3.5–4 mm. above corolla-base, 0.1 mm. long; gynobase ca. 1 mm. tall, pyramidal below the middle and attenuate above the middle, terminated by a style 2.5–3.5 mm. long; style shortly bilobed at the apex, each lobe bearing a subterminal stigma; stigmas somewhat oblique, most prolonged on abaxial side, at anthesis closely juxtaposed and apparently united, in age the short lobes of the style tending to spread and the stigmas to separate, sterile tips of the style-lobes broad convex, scarcely surpassing the stigma; nutlets cinereous or pinkish and frequently somewhat mottled with brown, somewhat verrucose or tumulose, 1.6 mm. long, 1.2 mm. broad, bent near the middle with the beaked upper half erect and paralleling the ventral keel and the broad rounded lower half horizontal and diverging from the ventral keel at an angle of about 90°, ventral edge of nutlet angulate, nearly straight and vertical, dorsal side of nutlet saddle-like, base of nutlet strongly constricted and substipitate bearing an oblique open more or less triangular areola ca. 0.5 mm. broad, areola apically constricted and prolonged as a narrow groove to about the middle of the prominent ventral keel.

Ranging in the deserts from eastern Morocco eastward into Egypt.

ALGERIA: Beni-Mora à Biskra, *C. Schmitt* 165 (G); environs d'Aïn-Sefra-Oranais, May 30, 1934, *Faure* (G). TUNISIA: Zarzis, May 1884, *Letourneau* (G); Oued Chaffar entre Ifax et Gafsa, 1904, *Romieux* 122 (G); Gabes (Kauzeria), in desertis, *Petard* 197 (G). TRIPOLITANIA: Souk-el-Djemâa, 1939, *Maire & Weiller* 1054 (G); Tripoli in sand near Tadjura, *Bornmüller* 824 (G); ad Sabratha, *Bornmüller* 823 (G); Tripoli near Gargaresik, *Bornmüller* 922 and 8246 (G). EGYPT: near Alexandria, Ramleh, *H. A. Hurst* (K).

6a. *Echiochilon fruticosum* var. *sieberi*, nom. nov.

Lithospermum divaricatum Sieber ex Spreng. Syst. 1: 543 (1825) — Ascalona, Palestine, Sieber.

Nutlets lance-ovoid, about twice as long as broad, 2–2.2 mm. long, 1–1.3 mm. thick, broadest above the rounded base and gradually narrowed towards the apex, back not saddle-like, venter angulate, nearly straight, vertical, bearing an ovate-lanceolate areola ca. 0.5 mm. broad on the ventral side of the rounded base, the apex of the areola gradually narrowing and prolonged upward along the ventral angle to above the middle of the nutlet.

Known only from Sinai, Palestine and Lebañon, on sands near the coast.

LEBANON: Jaffa, sables maritimes, Nov. 1832, *Bové* 224 (K), 428 (G, K); ISRAEL: Khan-Yunis, March 12, 1926, *S. Fishelsohn* 350 (K); Ascalona, in collibus arenosis, *Sieber* s.n. (Isotype, G, K); in planitie Philistaea at Chan-Junis (ad fines Aegypt.), May 27, 1897, *Bornmüller* 1171 (G, K). EGYPT: Sinai Desert, May 1916, *M. F. White* (K).

The oldest and best known species of the genus. It has been collected repeatedly in the deserts of North Africa, in all the states from Morocco to Egypt. For a widely distributed plant it is surprisingly constant. The

most conspicuous variation concerns the coloration of the calyx-lobes and the bracts of the inflorescence. These may be entirely green but usually tend to have a blue margin and because of their coloration can become very conspicuous. A form in which the blue calyx-lobes and bracts are margined with carmine red, thus giving the inflorescence a distinct reddish tonality, has been described from Tunis as the var. *marginata*.

The most important variation detected within *E. fruticosum* involves the shape of the nutlets. In plants ranging from Sinai northward along the Palestine coast, the var. *sieberi*, the nutlets are always lance-ovoid. The African plants, typical *E. fruticosum*, have bent nutlets. The longitudinal axis of the nutlet is not straight and vertical as in the nutlet of the Palestinian var. *sieberi*. It is medially bent 90° with the upper half vertical and the lower half horizontal and directed away from the axis of the fruit. In lateral outline the nutlets of typical *fruticosum* are sway-backed. The dorsal edge is not straight above the rounded base as in var. *sieberi* but incurving, sagging inward near the middle and suggesting a saddle in silhouette. In various genera of the family the nutlets have the body bent ventrally, towards the floral axis, cf. Jour. Arnold Arb. 35: 161 (1954), but dorsal bending, away from the axis, is rare and generally weak. The strong dorsally bent nutlets of *E. fruticosum* are perhaps unique in the family.

A careful description of the minor details of corolla structure is needed and should be prepared by someone with access to fresh material. On some corollas, below the middle of the large upper lip, I have observed a light-colored area upon which sand is usually found adhering. The area seems to bear numerous minute stipitate glands.

7. *Echiochilon arenarium* (Vatke), comb. nov.

Heliotropium arenarium Vatke, Linnaea 43: 319 (1882) — Type from Brava,

Ital. Somaliland, Hildebrandt 1314. Not *H. arenarium* F. v.M. (1867-68).
Sericostoma arenarium (Vatke) Johnston, Contr. Gray Herb. 92: 92 (1930).

Plant fruticose with numerous very leafy much-branched prostrate or widely spreading stems 5–25 cm. long; foliage and new growth somewhat succulent, bearing loosely to closely appressed, uncrowded hairs 0.3–0.9 mm. long which usually arise from mineralized discoid bases; leafy branches 1–10 cm. long, internodes 1–10 mm. long; leaves numerous, oblanceolate, 2–20 mm. long, thickish, more or less conduplicate and having involute margins, upper surface concave or frequently hidden by the infolded margins, lower surface convex, not costate, apex obtuse or rounded; inflorescence multiflorous, terminating the leafy branchlets, usually a short dense unilateral and biserrate racemose cyme, commonly 1–2 cm. long but sometimes short and glomerate; calyx at anthesis 2–3 mm. long, subsessile or with a stout pedicel 0.5 mm. long, lobes about equally long or moderately unequal, thick, united towards the base, bearing loosely appressed hairs arising from thickened bases, not costate, abaxial lobe usually tending to be broadest and even the longest; calyx in fruit 3–5 mm.

long, lobes usually thick; corolla apparently white, funnelform, 3–6 mm. long (usually 3–4 mm. long and only shortly surpassing the calyx), subcylindric below the middle, outer surface glabrous or sparsely hairy only on the lobes, limb 1.5–3 (–4.5) mm. broad; lobes ascending, equal or nearly so; throat inside bearing abundant white hairs; anthers 0.5–1 mm. long, usually included; filaments very short, equal, affixed at equal distances above the base of the corolla; gynobase pyramidal; style 1–3.2 mm. long, terminated by a pair of sterile attenuate lobes, lobes erect juxtaposed parallel slightly unequal in length, 0.2–0.5 mm. long; stigmas 2, forming the discrete halves of a pale, swollen, sometimes oblique, vesicular ring borne about the base of the bilobed sterile tip of the style; nutlets 1.2–2 mm. long, 1.0–1.7 mm. broad, thick, ovate in dorsal outline, obscurely tuberculate, back convex, venter obtusely angled, areole evident, obliquely basal, triangular or transversely elongate, abruptly contracted into a narrow lateral groove which is prolonged upward to above the middle of the nutlet.

Coastal dunes along middle and southern Italian Somaliland.

ITALIAN SOMALILAND: sand hills near Brava, March 1874, *Hildebrandt* 1314 (frag. of Type, G; Isotype, BM); Mogadiscio, dune stabile, Aug. 8–9, 1929, *L. Senni* 575, 596 (Fl); dintorni di Mogadiscio, *Ciferri* 66 (Florence); spiaggia di Mogadiscio, May 17, 1913, *G. Paoli* 5, 10 (Fl); Mogadiscio, nelle vicinanze del campo avicazione, April 9, 1939, *R. Corradi* 6335 (Fl); litorale di Ras Mallen, 1890, *R. Bricchetti* 512 (Fl); duna tra Magangib e Obbia, April 18–19, 1924, *Puccioni & Stefanini* 369, 382 (Fl).

A very distinct species with salient characters in the prolonged sterile tip of its style, the short tube of the calyx, the white faecal hairs in the corolla and the short not abundantly flowered inflorescences. The plant is a small shrub with succulent herbage. It frequents dunes along the coast of Italian Somaliland. The prolonged sterile bilobed tip of its style is of some interest, since the sterile tip and the stigma together form an aggregate which is very suggestive of the stigmatic head in *Heliotropium*. Indeed, because of this similarity the species was originally proposed as a species of *Heliotropium* and some recent authors have been content to continue to treat it so. A comparison of the style of *E. arenarium* with that of other species of the genus makes it very clear that these are all similar in structure and organization. In the present species the sterile tips of the style are simply more generously developed and more prolonged than in other congeners. The similarity to the stigmatic head in *Heliotropium* is superficial. The closest homologies, outside *Echiodhilon*, are to be found not in *Heliotropium* but rather in *Buglossoides* and *Lithospermum*, cf. *Jour. Arnold Arb.* 35: 161 (1954).

I have found abnormal flowers frequently developed on the herbarium specimens available to me. These flowers have corollas 6–9 mm. long. The tube, 4–6 mm. long and 1–1.5 mm. thick, is gradually narrowed upwards and then abruptly expanded into a campanulate or even hemispheric throat, 2.5–4 mm. long and 3–4 mm. thick. The corolla lobes are thick,

erect, rounded and 1.5–2 mm. long. The tissue of the tube and throat is heavily mineralized. Examination shows that such corollas are, or have been, inhabited by a hymenopterous (?chalcid) larva and are gall-like hypertrophies. They are especially well developed on *Hildebrandt* 1314, the original collection of the species. Monstrous flowers of similar nature have been observed in only one other species of *Echiochilon*, in *E. strigosum*, and then only in very limited numbers.

8. *Echiochilon jugatum*, sp. nov.

Herba perennis pilis abundantibus rectis valde appressis 0.2–0.5 mm. longis pallidis indumentum levum argentaceum formantibus vestita; caulinibus numerosis decumbentibus ascendententer ramosis 1–5 dm. longis 1–2.5 mm. crassis, internodiis 2–5 (–10) mm. longis; foliis numerosis omnino oppositis decussatis ascendentibus vel supra medium plus minusve recurvatis cernosis concavo-convexis 1.5–6 mm. longis utrinque dense strigosis nullo modo costatis, basi 1.5–3 mm. latis anguste 0.5–1.5 mm. lateque connatis; floribus oppositifoliis vel rarer axillaribus dissitis paucis apicem versus caulis ramorumque inter paria foliorum oppositorum gestis; calyce sessili sub anthesi 3.5–4.5 mm. longo, fructiferi ad 5 mm. longo, lobis saepe subaequilongis lanceolatis; corolla 5–6 mm. longa; limbo haud obliquo 5.5–7 mm. diametro; tubo (faucibus subcylindraceis inclusu) 3–4 mm. longo, intus basim versus inconspicue minutissimeque pubescenti; lobis patentibus aequalibus obtusis 2 mm. longis basim versus 2.5 mm. latis in faciebus utrinque albo-villulosis margine erosis; faucibus intus flavo-villlosis; antheris exsertis 1.3–1.9 mm. longis; filamentis 0.8–1 mm. longis, omnibus ca. 3 mm. supra basim tubi orientibus; gynobasi pyramidali 2–2.5 mm. longa basim versus ad 1.5 mm. lata; stylo 1.5 mm. longo apicem sterilem inconspicuum latum convexum stigmata horizontalia vix superantem proferente; nuculis ca. 3 mm. longis, 2 mm. latis, sublaevibus vel sparse verrucosis, cinereis vel rosaceis; cicatrice laterali verticali basi ad 1.5 mm. lata supra basim sursum abrupte deinde gradatim contracta.

Eastern Arabia, near the coast, from Bahrain Island south to Dhofar.

ARABIA: Bahrain Island, sandy desert at northwest end of pipeline, March 11, 1950, *Ronald Good* 224 (BM, K); Dubai, Trucial Oman, sand on limestone near sea level, plant 11–18 inches tall, leaves gray green, fl. pale yellow, March 22, 1937, *Mrs. F. Holmes* 351 (BM, K); Near Ras al Hadd, Gulf of Oman, sand dunes, Nov. 5, 1933, *H. Carr Gilson* K 10 (K); near Jazir, Wadi Ghudun, long. 56°45'E, "Halmit," Feb. 9, 1947, *W. Thesiger* (BM); Wadi Shibun, long. 56°00'E, "Halmit," Feb. 11, 1947, *W. Thesiger* (BM); Dhofar Mountains, Marbat, coast, 1895, *Mrs. J. T. Bent* 21 (Type, Kew); Red Sea, *Dr. Nimmo* (K).

The opposite leaves in *Echiochilon jugatum* are narrowly connate and accordingly arise from a short tight vaginate base. The flowers, usually borne opposite foliaceous bracts, occur along the terminal portion of the stems and branches and are usually separated by one to several pairs of leaves. There is no crowding of the flowers to form a differentiated race-

mose inflorescence. In other species of *Echiochilon* only the lowest leaves on the stem and branches are opposite, most of the leaves being alternate. In *E. jugatum* all the leaves are opposite. As to general facies I find the present species more suggestive of a member of the Caryophyllaceae or Chenopodiaceae than of the Boraginaceae. Among the members of *Echiochilon* the species most closely approaches *E. kotschy* in habit as well as in other characters.

The collection from the "Red Sea" by Dr. Nimmo, cited above, is one of a number with such data contained in the Hooker Herbarium at Kew. J. B. Balfour, Bot. Socotra pg. xvi (1888), believes that some of these actually originated on Socotra. Indeed on most of Dr. Nimmo's collections from the "Red Sea," a definite locality "Socotra" has been added in pencil by some person unknown. I do not believe that Nimmo's material of *E. jugatum* came from either the Red Sea or the island of Socotra. The plant is definitely known only from Bahrain Island and from other localities in southeastern Arabia not far from the coast in Trucial Oman and in Oman. Nimmo also has a collection of *E. thesigeri*, a species that has been found in this same section of Arabia. Of special interest is a collection of *Cynoglossum* at the British Museum from Jabal Qara, Dhofar (D. Vesey Fitzgerald 12448-4) which without doubt is conspecific with a collection of Nimmo (from "Red Sea") in the Kew Herbarium. Although at first I believed an undescribed species was involved, much to my surprise I find that the Arabian plant is indistinguishable from *Cynoglossum coelestinum* Lindl. of the mountains of Bombay State, India. For the matter at hand the important fact is that this very distinct *Cynoglossum*, long ago found by Nimmo, has recently been localized in Arabia where it appears to be native. The locality in the mountains overlooking the Dhofar Coast is in the same general area as that in which Bent collected *E. jugatum*. From what is known of the distribution of *E. thesigeri*, that species can be expected eventually to be found also within this same general area. It is quite possible that Dr. Nimmo collected all three of the Boraginaceae mentioned during a visit to Dhofar, probably while his ship was at anchor at Marbat.

9. *Echiochilon kotschy* (Boiss.), comb. nov.

Lithospermum kotschy Boiss. & Hohenack. ex Boiss. Diag. Pl. Orient. Nov. 4: 49 (1844); Boiss. Fl. Orient 4: 219 (1875) — Type from Karrak Island, Persian Gulf, *Kotschy* 15.
Sericostoma kotschy (Boiss.) Franchet in Révoil, Fauna et Flore Pays Comalis (Sertulum Somalense) 46 (1882).

Plant suffruticose, pale strigose; hairs of indument white, rigid, abundant, strongly appressed, 0.5-1 mm. long; stems becoming 3 dm. long, at base 3 mm. thick; leafy branchlets numerous, strict, slender, usually ca. 1 mm. thick and 5-10 mm. long, internodes 1-5 mm. long; leaves abundant, 2-4 mm. long, 0.8-1.2 mm. broad, oblong, usually loosely recurving, upper surface concave, lower surface convex, apex obtuse; leaves mostly alternate, only the several lowest pairs of leaves on the shoot opposite;

flowers oppositiflorous, borne interspersed among the leaves above the middle of the leafy branchlets, not aggregated into a well-defined inflorescence; calyx-lobes all about the same length, about 4 mm. long at anthesis, shorter than the corolla-tube; corolla 5.5–6 mm. long, with a moderately oblique limb 4–5 mm. broad, the 2-lobed adaxial side of corolla ca. 0.8 mm. longer than the abaxial side, tube about 1.5 mm. thick at base, ca. 2 mm. long, short-cylindric, expanding into a throat ca. 2.5 mm. broad at the summit; throat inside bearing abundant yellow hairs; corolla-lobes strigulose on both surfaces, broadly triangular-ovate, 1.5 mm. broad, 1.2 mm. long, ascending, medial abaxial lobes slightly smaller than the other four; anthers 1.7 mm. long, only the tip of the adaxial anther exserted; filaments unguiculate, ca. 0.5 mm. long, affixed at unequal heights in the corolla-throat, adaxial one arising ca. 3.5 mm. above corolla-base, dorsal lateral pair ca. 3 mm. above base, and anterior pair ca. 2.5 mm. above corolla-base; style 1.5–1.7 mm. long, with a very short truncate or convex sterile tip surrounded by the two lobed horizontal vesicular stigma; nutlets pinkish, 2–2.3 mm. long, 1.5 mm. broad, nearly smooth, obscurely tumulose, areola lateral and vertical, 1 mm. wide at base, abruptly narrowed into a groove which extends upward almost to nutlet-apex.

IRAN: Korgo (Khargu) Island, Persian Gulf, ca. lat. 29°00', in arenosis, Jan. 7, 1842, *T. Kotschy* 15a (G, K); Karek (Kharg) Island, Persian Gulf, Jan. 1842, *Kotschy* 15 (K, Isotype).

A plant growing in sand and known only from a group of small islands lying about 30 km. off the Iranian shore near the northern end of the Persian Gulf. Its relations are clearly with the Arabian *E. jugatum* and with *E. persicum* of Iran and Baluchistan. As in the species mentioned, the nutlets of *E. kotschyi* are nearly smooth and its indument is pallid. Our plant has noticeably more slender stems and leaves than *E. jugatum* and differs further in having most of its leaves alternate. *Echinochilon kotschyi* differs from *E. persicum* in inflorescence, zygomorphic corollas, small leaves and less roughened nutlets.

10. *Echinochilon vatkei* (Baker), comb. nov.

Heliotropium calcareum Vatke, Linnaea 43: 318 (1882), not Stocks (1852) —
Type from Yafir, Ahl Mountains, Brit. Somaliland, *Hildebrandt* 890a.
Heliotropium vatkei Baker in Thiselton-Dyer, Fl. Trop. Africa 4²: 39 (1905)
— a renaming of *H. calcareum* Vatke (1882), not Stocks (1852).
Sericostoma calcareum (Vatke) Johnston, Contr. Gray Herb. 92: 92 (1930).
Heliotropium thymoides var., sensu Vatke, Oesterr. Bot. Zeits. 25: 166 (1875).

Plant suffrutescent, 15 cm. tall; stems slender, numerous, ascendingly branched; leafy branchlets 1–5 cm. long, ca. 1 mm. thick, scantly strigose with stout straight hairs 0.5–1 mm. long, internodes 1–2 mm. long; leaves oblong to broadly oblanceolate, thickish, not costate, 2–5 mm. long, 0.5–0.9 mm. broad, mostly alternate, only the lowermost on the shoot opposite, bearing inconspicuous scattered stipitate glands, scantly strigose and bear-

ing some spreading hairs along the margin (hairs straight, 0.5–1 mm. long), upper surface concave, lower surface convex, apex rounded or obtusish; flowers borne opposite or lateral to a leaf at irregular intervals along the leafy (sometimes branching) ultimate twigs, not arranged in a well-developed, elongate unilateral inflorescence; calyx at anthesis 2–2.5 mm. long, in fruit becoming 4 mm. long and usually with a pedicel ca. 1 mm. long, lobes subequal, at anthesis ca. 2 mm. long, oblong or broadly spatulate; corolla 3.5–4 mm. long, funneliform, regular, limb 3–3.5 mm. broad, corolla-lobes ascending, 1.5 mm. wide, 1.0 mm. long, outer surface villulose-stribose, tube (including throat) 1–1.8 mm. long, throat densely yellow villulose inside; annulus represented by tufts of minute hairs borne in a band 0.3 mm. above corolla-base; filaments equal, 0.7 mm. long, arising at equal heights in the throat 1.5–1.7 mm. above the corolla-base, anthers 1.3 mm. long; style short, 0.6–0.7 mm. long, with a very short convex sterile tip; stigma 2-lobed; nutlets (only one developing) 2 mm. long, at base 1.5 mm. thick and 1.5–1.7 mm. broad, apex somewhat rostrate, surface somewhat reddish, verrucose; attachment-areole green, lateral, vertical, 0.5 mm. wide at base, abruptly narrowed upwards into a short groove, rarely prolonged above the middle of the nutlet.

BRITISH SOMALILAND: Yafir, Ahl Mts., 2000 m. alt., March 1873, *J. M. Hildebrandt* 890a (G, frag. of Type; BM, Isotype).

In having the flowers borne among the leaves along the outer portion of the leafy twigs and not in a well-defined, many-flowered unilateral racemose inflorescence, the present plant is distinguished from all other species known from British Somaliland. It is most closely related to *E. verrucosum*, from which it differs, in addition to the inflorescence, in having small leaves, a short style, and equal filaments all borne at the same height above the corolla-base.

The species is known only from the type collection obtained about Yafir, a broad pass near the crest of the Ahl Mountains, near long. $48^{\circ}30'E$, about 50 km. east-southeast of Las Gori, in extreme eastern British Somaliland. Under the incorrect name "*Heliotropium thymoides*," it is mentioned by Hildebrandt, *Zeitsch. d. Ges. f. Erdkunde, Berlin*, 20: 286 (1875), in the account of his visit to the Ahl Mountains.

11. *Echiochilon albidum* (Franchet), comb. nov.

Sericostoma albidum Franchet in G. Révoil, *Fauna et Flora Pays Comalis (Sertulum Somalense)* 46 (1882).

Leaves densely and completely clothed by an abundance of appressed straight clean white somewhat lustrous hairs ca. 1 mm. long; corolla 4 mm. long, apparently regular; filaments equal, ca. 0.5 mm. long, arising ca. 2.5 mm. above the base of the corolla.

SOMALIA: no locality given, *Geo. Révoil* 81 (Paris, Type).

A species known only from the type specimen which was collected at

some unrecorded locality in northeastern British Somaliland or in adjoining portions of extreme northern Italian Somaliland. George Révoil worked for a few days near Heis, but during most of his nine months in Somalia he travelled and studied in the area east and southeast of Las Khoreh (Las Gore), and as far eastward as Bargal on the shores of the Indian Ocean. At no time, however, was he ever more than 100 km. south of the shores of the Gulf of Aden, cf. G. Révoil, *La Vallée du Darror*, pp. 1-388, map, Paris, 1882.

I examined the type of the species at Paris but unhappily, except for the few details recorded above, my notes on the type have been lost. The plant seems to be most closely related to *E. verrucosum* of western British Somaliland. It differs in having a regular corolla with the stamens borne at equal heights on the corolla. Its most distinctive feature, however, is its dense indument of very abundant, very clean and white appressed hairs. A very few collections of *E. verrucosum* (e.g., Gillett 4026 from Hargesia) have a white indument but none of them has a snow-white or somewhat silvery white indument such as that possessed by the type of *E. albidum*.

Of the six species of the genus known from British Somaliland and adjacent extreme northern Italian Somaliland, only *E. verrucosum* is known from a goodly number of scattered collections. It appears to be widely distributed in the hills over the western half of British Somaliland and is there the only perennial representative of the genus. In the eastern half of British Somaliland and in adjacent Italian Somaliland the genus is represented by a number of apparently local species. Of the five occurring in this latter area (*E. arabicum*, *E. vatkei*, *E. collenettei*, *E. adenophorum* and *E. albidum*), only *E. arabicum* is known from more than a single station or has been collected more than once. The behavior of *Echiochilon* in eastern British Somaliland and in northern Italian Somaliland differs from that elsewhere within the geographic range of the genus. More species are concentrated in this area than in any other of comparable size. Also, the geographic distribution of the species of *Echiochilon* within the area is extremely localized as compared with those occurring elsewhere. Recognizing these facts, it seems wise therefore to accord at least conditional recognition to *E. albidum* until it has been recollected and more is known concerning the plant and its occurrence. If *E. albidum* is not a recognizable local endemic species of extreme eastern British Somaliland or adjacent Italian Somaliland, it may prove to be only a form of *E. verrucosum*. Should this be true, the name "albidum" being older than "verrucosum," the binomial *E. albidum* would become the correct one for the plant I have treated as *E. verrucosum*.

12. *Echiochilon strigosum* (Deflers), comb. nov.

Sericostoma strigosa Deflers, Bull. Soc. Bot. France 43: 120 (1896) — Type from southwestern Arabia, Bilad Fodhli, ad fauces australes montis el'Areys, 500-600 m. alt. Deflers 1075.

Heliotropium deflersii O. Schwartz, Mitt. Inst. allgem. Bot. Hamburg 10: 212 (1939) — based on *S. strigosa* Deflers (1896).

Plant suffrutescent, apparently prostrate; stems very slender and very loosely branched, 10–20 cm. long; leaf-bearing branchlets 5–12 cm. long, 0.5–1 mm. thick, densely strigulose (hairs 0.1–0.5 mm. long), with internodes 0.2–5 mm. long, bearing very numerous small leaves directly upon the branchlet and also in axillary fascicles; leaves linear or narrowly oblong, sessile, 1–6 mm. long, 0.5–1 mm. broad, becoming loosely but distinctly recurved, usually green, sparsely strigulose (hairs 0.1–0.8 mm. long) and sometimes sparsely ciliate (hairs 0.6–1.2 mm. long) below the middle, mostly alternate, with only the lowest 2–3 pairs on the shoot opposite; leaf-blade thickish, more or less conduplicate, the upper surface mostly hidden and apparently narrowed to a longitudinal groove, lower surface convex, not costate; inflorescence 10–20-flowered, unilateral, becoming loosely racemose, 1–7 cm. long, terminal on the branchlets; bracts small, linear, 1–2 mm. long; calyx at anthesis 1.5–2.5 mm. long, borne on a strict pedicel 0.5–1 mm. long, lobes linear, 1–2 mm. long, equal or nearly so, not costate; corolla 3–4 mm. long, unilaterally prolonged on the adaxial side, densely strigulose outside, limb moderately but distinctly oblique; corolla-lobes about equal, ca. 1 mm. diameter, usually with pale crisped margins, two rear lobes overtopping the other lobes 0.5–1 mm.; corolla-throat with abundant yellow hairs inside; annulus marked only by an indistinct inconspicuous band of minute hairs ca. 0.5 mm. above the corolla-base; anthers 0.7–0.9 mm. long, sometimes exserted; filaments unequal, 0.5–1.5 mm. long, arising at unequal heights above the corolla-base, one 1.5 mm. above the base, two ca. 1.8 mm. above the base and the remaining two 2–2.1 mm. above the corolla-base; gynobase broadly pyramidal; style 0.5–1.2 mm. long, the sterile tip convex, short; stigmas 2; nutlets 1.5–2 mm. long, above the base 1.5 mm. wide and 1.2–1.5 mm. thick, commonly 3–4 developing, back verrucose or somewhat papillate, venter with prominent scar and keel, attachment-scar lateral and vertical (or perhaps sometimes somewhat oblique), ca. 0.5 mm. broad, ovate or broader than long; groove closed or a narrow prolongation of the areola extending up to the middle of the nutlet.

Known only from the western half of the south coast of Arabia.

ARABIA: Montes el'Areys, Bilad Fodhli, 500–600 m. alt., April 28, 1893, *A. Deflers 1075* (Paris, Type; G, fragment); hills near Dobaibah [35–40 mi. east-northeast of Mukalla], Hadhramaut, small plant, flowers pale blue, 3000 ft. alt., Feb. 28, 1894, *W. Lunt 224* (K); between Mukalla and Sai'un, jol along East Road, Hadhramaut, March 30, 1952, *G. Popov 530* (BM).

Among the distinctive features of *E. strigosum* are its very slender and very loosely branched stems, its very short, narrow, usually recurved leaves and its abundant, frequently crowded, axillary fascicles of leaves. On some plants the well-developed leaf-fascicles are so numerous and so crowded as to form a cylindric mass of foliage 7–8 mm. in diameter that completely hides the twig within it. The species is a well-marked one, having its closest relations perhaps in *E. verrucosum* of British Somaliland.

Deflers appears to have collected the type of species in what is now known

as Dairi, Fadhli Sultanate, in the Aden Protectorate about 45–50 miles north-northeast of Aden. His collection is unquestionably conspecific with those I have cited from the Hadhramaut.

13. *Echiodchilon persicum* (Burmann f.), comb. nov.

Heliotropium fruticosum var. *persicum* Burmann f., Fl. Indica 41, t. 19, f. 1 (1768) — Persia.

Heliotropium persicum Burmann f. Fl. Indica t. 19, f. 1 (1768); Lam. Encyc. 3: 94 (1789).

Sericostoma persicum (Burm. f.) B. L. Burtt, Kew Bull. 1949: 138 (1949).

Lithospermum persicum Gand. Bull. Soc. Bot. France 65: 62 (1918) — “Persia merid., Laristan ad Bender-Abbas (Bornmüller No. 521!).”

Lithospermum kotschyi var. *brevifolia* Bornmüller, Mitt. Thür. Bot. Vereins n.s. 6: 59 (1894) — “bei Bender-Abbas am Fusse des Kuh Ghino gesammelt,” J. Bornmüller 522, in pt.

A decumbent shrub with pallid herbage; old stems lignescent, as much as 8 mm. thick; leafy branchlets 5–15 cm. long, 1–2 mm. thick, simple or ascendingly branched above the middle, pallid strigose (hairs straight 0.5–1 mm. long, closely appressed), internodes 1–10 mm. long; leaves pallid-strigose and usually also more or less coarsely ciliate (hairs straight 0.5–1 mm. long), usually ascending, 3–15 (usually 5–10) mm. long, oblong or oblanceolate, 1–3 mm. broad, thickish, weakly conduplicate or the upper surface merely somewhat concave, lower surface convex, not costate; lowest 2–3 pairs of leaves on the shoot opposite, the others all alternate; inflorescence bracted, unilateral, 10–20-flowered, racemose, 3–8 cm. long, terminating the leafy shoots and their branches; bracts oblong, shorter than the calyx; calyx at anthesis 3.5–4 mm. long; lobes 2.5–3 mm. long, equi-long or nearly so; corolla 4.5–6 mm. long, tubular funnelform, abaxial side 1–1.5 mm. shorter than the adaxial side, outer surface minutely villulose; limb 4–6 mm. in diameter, moderately but distinctly oblique; corolla-lobes ascending, 1–1.5 mm. diameter, margins crisped, medial abaxial one slightly but perceptibly the smallest; throat inside bearing abundant yellow hairs; annulus usually marked only by an indistinct band of minute hairs ca. 0.5 mm. above corolla-base; anthers 1.2–1.7 mm. long, usually included; filaments 0.5–0.8 mm. long, unequal, borne at unequal heights (2.3–3 mm.) above the corolla-base; style 0.9–1.5 mm. long, sterile tip very short, low-convex; gynobase 1.5 mm. tall, abruptly narrowed above the broad (ca. 1 mm.) base; nutlets 2–2.3 mm. long, above the base 1.5–1.7 mm. broad and 1.3–1.6 mm. thick, gray or pinkish, usually one or more aborted, back convex, obscurely roughened or tumulose and with a few scattered prominent tuberculations; areola green, vertical (or rarely somewhat oblique), ca. 1 mm. broad, abruptly contracting into a narrow groove extending upward to above middle of the nutlet.

Known only from the coastal areas of southern Iran and Baluchistan.

IRAN: Henjam Island, Strait of Hormuz, W. Wykeham (K); sand hills near Bandar Abbas, Jan. 19, 1893, J. Bornmüller 521 (G); near Gahkum, lat. 28°11'N,

long. $55^{\circ}50'E$, woody shrub 2 ft. tall, fl. brownish purple, silty plain, 3000 ft. alt., March 25, 1951, *G. B. Popov* 46 (BM, G); Makran (perhaps near Jask, long. 58°), *Aucher-Eloy* 5001 (K, P); Tcharbahar (Chahbar), Tiss, long. $60^{\circ}40'$ June 12, 1943, *A. Parsa* (K). PAKISTAN: Hala Range, long. $66^{\circ}E$., *Capt. Vicary* (K).

This species is the oldest in the genus. It was first described and figured nearly two hundred years ago from a plant said to have come from Persia. Unfortunately it was mistakenly identified with *Heliotropium*. Only recently was the true identity established by B. L. Burtt. This plant is the most easterly ranging member of *Echiochilon* and the only one known from the mainland of Iran or from Pakistan to the eastward. Its closest relation appears to be *E. kotschyi* of the islands of the Persian Gulf. The insular species, however, is very distinct, differing from *E. persicum* in its practically smooth nutlets, few-flowered inflorescence, small recurved leaves and its regular, rather than zygomorphic corollas.

14. *Echiochilon arabicum* (Schwartz), comb. nov.

Tetraedrocarpus arabicus O. Schwartz, Mitt. Inst. allgem. Bot. Hamburg 10: 212 (1939) — southern Arabia (Hadramaut), near Mukalla, *Wissmann* 1241; on mountainsides behind Mukalla, near Lasb, *Wissmann* 1240; in the Wadi Himen, *Wissmann* 1234.

A small slender-stemmed grayish green shrub 1–5 dm. tall, hispid, loosely or densely branched; leafy branchlets 5–20 cm. long, 1–1.5 mm. thick, internodes 1–10 mm. long; older branches distinctly shrubby, 3–5 mm. thick, usually decorticating; leaves oblanceolate, all alternate or only the lowest pair on the shoot opposite, 5–15(–35) mm. long, from a narrow base gradually broadening and becoming 1–4 mm. broad between the apex and the middle, apex acutish, firm, thickish, weakly conduplicate, lacking midrib and veins, bearing stiff (even pungent) straight hairs 0.7–1.5 mm. long which arise from discoid bases, hairs loosely appressed or those along the leaf-margin more or less spreading; inflorescence elongating, racemose, unilateral, 10–40-flowered, becoming 5–17 cm. long; calyx 2–2.5 mm. long at anthesis, becoming 3–5 mm. long in fruit, base narrowed into a strict pedicel 1–2 mm. long, lobes about equally long but with the abaxial one broadest, without evident midrib; bracts numerous, mostly small and not surpassing the calyx; corolla 5–8 mm. long, funnelform, prolonged on the adaxial side, minutely hispidulous or villulose outside, tube 3–5.5 mm. long and 1–1.5 mm. thick expanding into a throat 2.5–3 mm. broad, limb distinctly, although only moderately oblique, sloping 25° – 35° from the horizontal; lobes prominently and dichotomously veined, inner surface sparingly white hairy above the base, the two adaxial lobes largest 2–2.5 mm. broad and 1.5–2 mm. long, medial abaxial lobe 1.5 mm. wide and 1 mm. long, anterior lateral lobes 1.7 mm. broad and 1–1.5 mm. long; corolla-throat bearing yellow hairs inside; anthers 1–1.2 mm. long, included or only shortly exserted; filaments borne at unequal heights above the corolla-base; medial adaxial filament 1–1.2 mm. long, arising 3–4 mm.

above the corolla-base; anterior pair of filaments 0.2–0.5 mm. long, arising 2–3 mm. above corolla-base; gynobase 2 mm. tall, attenuate, abruptly arising from a broad base, 1.5–2 mm. high, ca. 1 mm. wide at base; style 1.2–1.5 mm. long, sterile tip very short and broad, stigma not oblique; nutlets 1.5–2 mm. long, above the base 1.3–1.5 mm. broad and 1–1.5 mm. thick, usually verrucose, gray or somewhat reddish, 1–4 developing; areola green, base broad and more or less oblique, usually triangular (ca. 0.8 mm. broad and 0.4 mm. long), prolonged upward on the vertical ventral angle of the nutlet as an open groove reaching almost to the nutlet-apex.

ARABIA: (Hadhrmaut): Mukalla, 1931, *H. v. Wissmann* 1241 (G, fragment of Type); Lasb [mountain slope back of Mukalla], May 1931, *H. v. Wissmann* 1240 (photo); el Sibeth [ca. 20 mi. north of Mukalla], 600 ft. alt., small straggling plant, flowers pale blue, Dec. 26, 1893, *W. Lunt* 94 (BM, K).

BRITISH SOMALILAND: Serrut Mts., inland from Mait, limestone, fl. pale blue, 1800 m. alt., April 1875, *J. M. Hildebrandt* 1416 (BM); Daageg delta, Heis, Erigavo Dist., fl. blue, bunch plant with thick taproot, Feb. 18, 1945, *Glover & Gilliland* 715 (BM, K); Dubriet Mt., lat. 10°22'N, long. 45°10'E, 500 m. alt., fl. pale blue, open sandy soil, *J. B. Gillett* 4776 (K, Fl).

Among the small-flowered members of the genus (spp. no. 7–17) the present one has the corollas which are most evidently zygomorphic and those which attain the largest size. The plant has relatively coarse foliage and has a thin open indument of loosely spaced, stiff, spreading or appressed hairs. It is, accordingly, a gray-green hispid plant and is more scabrous than other congeners. Because of these details I find the plant as to gross aspect very suggestive of the American genus *Cryptantha*.

In Arabia the species has been collected near Mukalla (the type locality) and also north of that port along the road to Wadi Hadhrmaut. Two congeners have also been found in this general area, *E. strigosum* and *E. thesigeri*. Like *E. longiflorum*, the present species is known from southern Arabia and also from the adjacent African mainland. It occurs in the coastal mountains of middle British Somaliland, in an area in which the genus is otherwise represented only by the very different *E. longiflorum*, *E. adenophorum* and *E. vatkei*.

The present species was based by Schwartz on two collections. Through the kindness of Dr. Walter Domke of the Institut für allgemeine Botanik, Hamburg, I have had available for close study an excellent photograph of the type of the species, as well as a very generous fragment of the cotype. It has been possible, therefore, to identify Schwartz' proposed new genus and species with certainty, an operation impossible had I been forced to depend completely on the rather ambiguous original description.

15. *Echiochilon nubicum*, sp. nov.

Fruticulus decumbens pallidus 10–15 cm. altus e radice lignosa valida palari ad 13 mm. crassa erumpens pilis abundantibus albis ca. 1 mm. longis appressis vestitus; ramis vetustioribus lignosis 2–5 mm. crassis decorticatis prostratis vel laxe ascendentibus; ramulis hornotinis erectis vel ascendentis

bus 5–15 cm. longis pallide strigosis saepe ascenderter ramosis foliosis 1–2 mm. crassis, internodiis 3–12 mm. longis; foliis oblongis vel saepissime oblanceolatis 7–14 mm. longis, 1–2.5 mm. latis alternis (vel solum eis basim versus ramulorum gestis oppositis) indumento pallido vestitis, supra concavis, subitus convexis haud costatis, margine crassis sparse hispido-ciliatis; inflorescentia ramulos foliosos terminanti 3–9 cm. longa densa unilaterali racemosa 10–20-flora bracteis obovatis vel obovato-oblongis instructa; calyce sub anthesi 2–2.5 mm. longo maturitate 2.5–2.9 mm. longo subsessili vel pedicello ad 0.5 mm. longo donato; lobis aequalibus oblongis maturitate apicem nucularum paullo superante; corolla 3–4 mm. longa extus minute villulosa, limbo ca. 3.5 mm. diametro horizontali, lobis homomorphis patentibus 0.8–1 mm. longis rotundis; faucibus intus flavo-villosis; tubo intus fere ad basim glabro vel annulo villuloso donato; antheris 0.9–1 mm. longis exsertis; filamentis aequalibus 0.3–0.5 mm. longis omnibus pari altitude (2–2.5 mm.) supra basim corollae affixis; gynobasi 1.2–1.5 mm. alta basi 1–1.3 mm. diametro deinde sursum abrupte contracta faciebus excavata; stylo 0.5–0.8 mm. longo supra stigmata horizontalia apicem sterilem inconspicuum perbrevem proferente; nuculis 1.7–1.9 mm. longis 1.5 mm. latis, 1.3–1.5 mm. crassis sparse irregulariterque sed prominenter tumulosis et verrucosis, dorso obtusis carina imperfecta tuberculata donatis; cicatrice laterali prominenti basim versus 0.7–1 mm. lata supra medium nuculae apicem attenuatum producta.

SUDAN: Macaur [= Makawa] Island, Red Sea, lat. 21°, 1864, *G. Schweinfurth* 2108 (Type, Kew); Nubia, about lat. 21°, seacoast between 3000 and 4000 ft. alt., 1896, *J. T. Bent* (K).

A plant known only from the middle of the west side of the Red Sea. Because of its pallid indument I find it most suggestive of *Echiochilon persicum* as regards gross aspect. Its relationship, however, seems to be closest with *E. verrucosum* of British Somaliland and perhaps also with *E. thesigeri* of Arabia. Among the features of the plant useful in recognizing it are its white indument, stout sessile or subsessile calyces, small regular corollas, and very short style.

16. *Echiochilon verrucosum* (Beck), comb. nov.

Sericostoma verrucosum Beck in P. Paulitschke, Harar 457, f. 3–6 (1888) — Type from Wárabot, western Brit. Somaliland, ca. 10 km. south of Zeila, *von Hardegger & Paulitschke*.

Heliotropium albo-hispidum Baker in Thiselton-Dyer, Fl. Trop. Africa 4²: 39 (1905) — Type from Hammar, Golis Range, Brit. Somaliland, Feb. 9, 1895, *Edith Cole*.

Small usually gray-green shrubby plant; older stems lignescent, prostrate or decumbent, becoming 5 mm. thick; leafy branchlets cinereous, erect, 2–15 cm. long, ca. 1 mm. thick, somewhat strigose (hairs 0.6–1.2 mm. long), simple or ascendingly branched above the middle, internodes 1–10 mm. long; leaves linear or linear-oblanceolate or sometimes oblanceolate, numerous 5–15 (usually 8–12) mm. long, ascending, 0.5–1 or sometimes

1.5 mm. broad, clothed with slender appressed hairs 0.5–1 mm. long, upper surface concave, lower surface convex, margin thick and usually sparsely hispid-ciliate; inflorescence terminating the leafy branchlets, erect, bracted, racemose, unilateral, 10–40-flowered, 5–14 cm. long; calyx at anthesis 2.5–3 mm. long, lobes linear or lanceolate, usually equal or nearly so but sometimes with the abaxial lobe enlarged; calyx in fruit somewhat crescent, with stout ascending pedicel 0.8–1.5 mm. long; corolla 4–5 mm. long, outer surface strigulose or villulose, limb 3.5–5 mm. in diameter, symmetric or obscurely prolonged on the adaxial side, lobes usually equal or practically so, rounded, 1–1.5 mm. broad and ca. 1 mm. long, throat yellow-villlose inside, annulus not differentiated, glabrous; anthers 1–1.2 mm. long, shortly exserted; filaments slightly unequal, 0.5–0.7 mm. long, affixed at unequal heights (at 2.4–2.5 mm., 2.6 mm. and 2.8–3 mm.) above the corolla-base; gynobase ca. 1 mm. broad at base, abruptly narrowing upward, 1–1.5 mm. high, faces excavated; style 1–1.3 mm. long, the sterile tip very short and convex, somewhat emarginate, scarcely surpassing the horizontal stigmas; nutlets usually rosaceous, 1–4 developing, verrucose or tuberculate, sometimes prominently and irregularly so, 1.8–2 mm. long, 1.5 mm. broad, 1.2 mm. thick, areola frequently green, lateral and vertical and tending to be prominent, from a broad base narrowing into an open groove extending upward towards the nutlet-apex.

Western British Somaliland, long. 43°00' to 45°15'E.

BRITISH SOMALILAND: Upper Sheik, long. 45°15'E. 1896–7, *Mrs. E. Lort Phillips* (BM); Daganeh, 2000 ft., small shrub on rocks, May 30, 1949, *P. R. O. Bally* 7266 (K, A); Golis Range, *Drake Brockman* 229, 246 (K); Hammar, Golis Range, Feb. 9, 1895, *Edith Cole* (Kew, Type of *H. albo-hispidum*); Adad-leh, Habrawal, long. 44°40'E. Feb. 20, 1899, *A. Donaldson Smith* (BM); Adda Gallah, April, *James & Thrupp* (K); Lafarug, April, *James & Thrupp* (K); Deragodle, in glareosis siliceis, Dec. 7, 1892, *D. Domenico Riva* 257/13 (Fl); north of Hargeisa, 4800 ft., fl. cream, top of limestone hill, *J. B. Gillett* 4026 (K, Fl); Afard, long. 44°8'E. 2000 ft., fl. white, schist slope, Oct. 24, 1932, *Gillett* 4448 (K); Dobo Pass, long. 43°15'E., 4000 ft., May 2, 1933, *Gillett* 4959 (Fl); betw. Gildessa and Zeila, 1889, *R. Bricchetti* 37 (Fl).

From this plant of western British Somaliland the other small-flowered Somalian species are easily separable, *E. arenarium* by its style, *E. vatkei* by its inflorescence, *E. arabicum* by its coarser habit and larger, strongly zygomorphic corollas, and *E. albidum* by its dense, very clean, lustrous white indument. As mentioned in my discussion of *E. albidum*, that species is imperfectly known. Its relationship to *E. verrucosum* must remain in doubt until new collections of it become available for study and comparison.

17. *Echiochilon thesigeri*, sp. nov.

Fruticulus ad 4.5 dm. altus cinerascens; ramis vetustis decumbentibus lignescens 2–7 mm. crassis decorticatis; ramulis hornotinis foliosis 5–15 cm. longis 1–1.5 mm. crassis saepe ascenderter ramosis sparse strigosis

(pilis 0.5–1 mm. longis rectis valde appressis) internodiis 2–10 mm. longis; foliis 2–12 mm. longis 1–2 mm. latis oblongis vel oblanceolatis sparse strigosis plerumque alternis solum eis fere ad basim ramulorum gestis oppositis, supra concavis, subtus convexis haud costatis, margine crassis sparse hispido-ciliatis; inflorescentia 10–20-flora racemosa unilaterali 2–8 cm. longa ramulos foliosos hornotinos terminante, bracteis oblongis plerumque minus quam 3 mm. longis; calyce ad anthesin 2.5–3 mm. longo, maturitate 0.5–1.5 mm. longe pedicellato, lobis equalibus vel subaequalibus 2–3 mm. longis; corolla 3.5–5.5 mm. longa extus plus minusve villulosis, limbo 4–5 mm. diametro horizontali, lobis ca. 1 mm. longis et 1–1.5 mm. latis rotundis equalibus vel subaequalibus, faucibus intus abundanter flavovillosis, tubo ca. 0.5 mm. supra basim inconspicue villuloso; antheris breviter exsertis 1–1.4 mm. longis; filamentis aequilongis ca. 0.5 mm. longis omnibus pari altitudine (1.6–3 mm.) supra basim corollae affixis; gynobasi basi 1–1.5 mm. lata deinde sursum abrupte attenuata 1–1.5 mm. alta; stylo 0.9–1.4 mm. longo supra stigmata horizontalia apicem sterilem truncatum perbrevem vel subnullum gerente; nuculis rubicundis ca. 2 mm. longis 1.5 mm. latis et crassis irregulariter et saepe prominenter verrucosis, dorse obtusis imperfecte carinatis; cicatrice laterali verticali viridi ovata supra medium nuculae sursum in sulco producta.

ARABIA: Bahrain Island, Persian Gulf, stony desert south of rifle range south of Safral, March 14, 1950, *R. Good* 223 (K); Jabal Hafit, Oman, April 25, 1948, *W. Thesiger* (Type, Brit. Mus.); wadi ascending to jol behind Zamuk, 3400 ft., drainage runnels in sand, intricate shrublet 8–18 in. tall, fl. white and crimson with yellow eye, Feb. 27, 1952, *Popov, Tillin & Gilliland* 4212 (BM); on northern jol near Zamuk, 4000 ft. alt., gravelly drainage runnels, intricate rough-hairy shrublet 8–12 inches tall, fl. white becoming blue-purple with yellow hairy throat, Feb. 28, 1952, *Popov, Tillin & Gilliland* 4220 (BM); "Red Sea," *Dr. Nimmo* (K).

This plant of eastern and southern Arabia has a habit at times closely simulating that of *E. persicum* of Iran and especially *E. verrucosum* of British Somaliland. From both these species, however, it is readily distinguished by having the stamens all borne at the same distance above the corolla-base and by having a corolla with lobes that are equal or practically so and a limb that is not oblique. In addition to *E. thesigeri* the genus is represented in Arabia by *E. jugatum*, *E. strigosum* and *E. arabicum*, all three very well marked and readily recognizable species.

Among the five collections cited, that from Bahrain Island appears to be a plant from an unusually rigorous situation. Though it has very short stems and very small leaves, it seems to be otherwise characteristic of the species. One of the collections (No. 4220) from near Zamuk [apparently a locality northwest of the Wadi Hadhramaut] is typical except for the fact that some minute stipitate glands are present on the calyx and along the younger stems. The glands, however, are inconspicuous and to be seen must be searched for. They are not conspicuous and should not cause the plant to be confused with the abundantly glanduliferous *E. adenophorum* and *E. collenettei* of British Somaliland.

